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FIGURES IN THE TEXT

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TROPICAL SOIL-VEGETATION CATENAS AND MOSAICS

A STUDY IN THE SOUTH-WESTERN PART OF
THE ANGLO-EGYPTIAN SUDAN

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(With Plates 1–17, containing Phots. 1–36, one Map, one Folding
Figure, and two Figures in the Text)

Foreword. This study is based on ideas gradually developed with the experience I have been able to acquire on several African journeys, reinforced by the contributions, written and in discussion, of other pedologists acknowledged in the text. It became clear, however, that an effective attack on the problems involved could only be made by a team able to study soils and vegetation conjointly. Work of this kind requires the complete co-operation of all concerned, and while I was responsible for the organization of the expedition, the general plan of the work and the specialist soil data, it has fallen to my younger colleagues to weave the mass of field observations, largely recorded by them, into a coherent whole. I wish to acknowledge the careful and detailed work they have done in carrying out this task.   C.G.T.M.

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I. INTRODUCTION

There are regions of Africa, quite apart from deserts, where the landscape is notable to the casual glance chiefly for its 'endless monotony'—a property, it should be added, which does not invariably mean unattractiveness. Only the most unobservant would say that the scene lacks variety of any kind; the monotony consists rather in the repetition of the same limited series of changes over huge tracts of country.

These repeated changes, or more correctly differences, are our concern in this paper. The 'huge tracts of country', as represented in many parts of the continent, may here be related to our own scene of operations by two examples differing only in degree. First it may be recalled that the southern Sudan† and the northern part of the Gold Coast, over 3000 km. apart, bear vegetation so similar, not only in general aspect but also in specific composition, that were samples of their vegetation placed side by side, the differences would still be hard to notice. If, secondly, we crossed the equator and compared a sample from, say, Northern Rhodesia, the difference in plant species would be evident, but the same general aspect and pattern of country would be found once more.

We are dealing, therefore, with phenomena of local differences which, although studied in a particular region, can be matched more or less closely over enormous expanses of Africa. Rather than extend our comparison to other continents as well, we may turn to more detailed matters.

The south-western Sudan was visited for three months in January–March 1939, by the authors of this paper and Mr J. E. Mansfield, with the purpose of studying the soil and vegetation types and their relationships. The expedition was made possible by generous financial aid from the Sudan Government, the Percy Sladen Trust, the Christopher Welch Trust (Oxford University), the Imperial Forestry Institute, and Balliol College. The scope of its activities depended upon the help and facilities provided in many ways by the Sudan Government and their District Commissioners in several places, and further help was given by their scientific staff. In particular, we had the advantage of travelling and

† Anglo-Egyptian Sudan to be understood throughout.

consulting, on more than one occasion, with the late Dr J. G. Myers, then Government Economic Botanist, a generous companion who was gifted with extraordinary aptitude for work in the field.

The three months occupied by the investigation were in the dry season, so that direct observation of the incidence of rains and floods could not be made and the herbaceous flora is by no means completely recorded. Two previous visits to the area had been made by Morison, on the first occasion with Messrs J. E. Dandy and D. Skilbeck, and on the second with Dr H. Greene, and the present paper takes cognizance of his earlier findings. The account which follows represents, however, our own analysis of the data collected on the 1938-9 expedition. The final form of the paper owes much to constructive criticism by colleagues and other friends with experience of similar country.

Soil samples and a few soil monoliths are preserved in the Soil Science Laboratory at Oxford, where the analytical work was carried out under Morison's direction by Miss E. Nussbaum, Mr D. V. Crawford and Mr P. Benham. Plant specimens were gathered in all regions visited, forming a collection covering a wider flora than that quoted in the present paper. The woody plants are deposited at Oxford, and the full set of herbaceous material is destined for the British Museum (Natural History). Beyond stating that every precaution was taken to secure reliable specimens and naming, particulars of this collection need not be given here. Our thanks should, however, be recorded for the help received from the British Museum (Natural History), where the herbaceous plants were identified, mostly by Mr J. E. Dandy and Mr E. G. Baker, and where the Combretums were named by Mr A. W. Exell. All the other woody specimens were named by Hoyle. Thanks are also due to Mr C. E. Hubbard of the Royal Botanic Gardens, Kew, for naming many of the grasses. We are grateful to Mr Dandy for criticizing the nomenclature of the whole list.

Capitals have been omitted throughout the paper from all specific epithets, and authorities are not quoted. The latter are given in a general list of species cited (Appendix, p. 81). This list also includes such synonymy as seems desirable in view of recent changes of names, especially of those used in the *Flora of the Sudan* (Broun & Massey, 1929). Where we are concerned in this paper with only one species of a genus, this species is usually quoted in the text by the generic name only, but the index gives the complete name.

Grateful acknowledgement is due to Miss M. Talbot and Mr L. Clinkard for their willing assistance in the preparation of the typescript and photographs.

THE PROBLEM

Before describing the scene of the investigation and the results obtained, it is necessary to outline the problem and explain the general thesis on which the data have been interpreted.

The problem is broadly as follows. In the savanna-woodland belts of tropical Africa, the conditions of occurrence of soil and vegetation types belonging to the highest categories (generalized groupings such as wooded ridges with red soils and valley grasslands with grey soils) have been readily recognized. Types subordinate to these, however, down to the lowest categories (closely defined groupings such as, say, shallow gravelly red soil bearing a society of the small tree *Hymenocardia acida*) very often occur as a confused, haphazard-looking patchwork of types. Soil-type units or plant communities of these lowest categories may be extensive or may cover only a few square metres. Over a large tract of

country, each type is recurrent, interspersed with the other types. Only when these lowest soil and vegetation units have been recognized does it become apparent that the recurring units of a given soil type repeatedly carry corresponding units of substantially the same plant community, so that soil-vegetation units exist as very real entities. But the presence of these soil-vegetation units in particular places, and their mutual relationships, appear at first almost fortuitous.

The two stages in understanding such an ecosystem—first the recognition in the field of the fundamental units, and secondly the appreciation of their relationship to each other and to controlling factors—are, in our experience, attained only through the adoption of the following general thesis. It represents an integration of certain fundamental facts and ideas, generally accepted or frequently put forward, but not often related consciously and logically either to each other or to the distribution of discrete soil-vegetation units. The sense in which certain terms are used is explained on pp. 6 and 7.

GENERAL THESIS

With certain limitations indicated below (p. 6), *the development of the soil on any site is mainly determined by the local topography†* *through its effect on water-movement.* The results are most striking in medium-rainfall areas in the tropics, especially where slopes are not very abrupt, and where parent material is uniform.

Three main soil complexes are so determined on the three main types of site:

(i) High-level areas have soils which may be grouped as the *eluvial* (E) complex. They are described as eluvial because the dominant feature is the eluviation of the soil profile either by downward movement of dissolved and suspended material in the soil horizons, or by the washing away of particles from the surface (erosion). The site as a whole represents the climatic normal in the sense that the soil receives neither water nor dissolved nor suspended matter from other areas, although there are, of course, many places within the complex which gain some material, and others which lose, depending on micro-relief, which may produce zonal or mosaic complexity.

(ii) Slopes are necessarily affected by the passage of water and solutes and also act as a sorting ground for such suspended particles as have been eroded from above. The soils formed from the material which remains on the slope constitute the *colluvial* (Col) complex.

(iii) Low-level areas receive such dissolved or suspended colluvial material as is not held up on adjacent slopes and, because of their position, lose little or none of it. Where they are, or have been, subject to a general valley or plain flood, the alluvial material brought from a distance by this means forms an added and often predominant component of their soils, whose development is largely controlled by the flooding or waterlogging characteristic of the site. Such soils together form the *illuvial* (Il) complex. The relative proportions of alluvial and colluvial material depend on local and general topography and rainfall. In wide, low-level areas with little general slope, the effect of micro-relief is very important.

Such a topographical sequence of soils has been given the useful name *catena*, which

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† The word 'topography', strictly meaning the study or description of places or districts, is used throughout this paper to mean relief, contour, configuration or lie of the land, on a larger or smaller scale. This usage follows a modern corruption of the original meaning, and seems unavoidable, since no other satisfactory word is provided with a corresponding, and frequently required, adjective which could replace 'topographical'.

is here used in the sense originally defined by Milne (1935). His posthumously published report (1947) gives further examples of catenas in Tanganyika. They clearly bear a strong general resemblance to examples in the Sudan. For the present, however, no attempt will be made to compare our findings with the numerous observations left on record by Milne. The catena concept has also been employed by Greene (1939, 1945) with reference to Sudan soils, and by Thomas (1945) in his account of hillsides in Uganda. Our basic classification of sites into high-level, slope and low-level is the same as that of Greene.

The vegetation which develops on these three main types of site, being closely correlated with the soils, likewise follows the form of a catena, and the detail of the vegetation within any one of the sites is, like the soil pattern, complicated by micro-relief. The eluvial soils generally occur in the form of a mosaic, or sometimes in zones, of phases differing in depth, and the vegetation on them closely follows the soil pattern. The colluvial soils, necessarily, are zoned, from coarse at the top of the slope to fine at the bottom, and bear more or less defined belts of vegetation parallel to the contour. The illuvial soils and their vegetation are in some places zonally arranged and in others they form a mosaic, according to the micro-relief.

It should be emphasized that although the three main types of site, each with its subdivisions, occur on three main topographical levels within a general drainage system, they are by no means always displayed in an easily recognizable, zonal manner. On a relatively large scale of local topography the sequence of the complete catena may be confused where a ridge and slope are succeeded by further undulations before any noteworthy drainage course or flood-plain is reached; or there may be undulations on the low levels of a flood-plain margin before any continuous rise to the higher eluvial levels. Confusion of the catenary sequence in such a way may be visualized more clearly from an actual example described later (p. 66). Surface relief of this undulating kind, on a scale larger or smaller in extent and elevation, produces a mosaic of areas situated at different levels. On the small scale some of these areas may be very restricted; within the eluvial or illuvial complex a unit of the mosaic may cover only a few square metres, and at least one of the colluvial zones is commonly only a few metres wide.

The often very complicated soil- and vegetation-mosaic thus resulting from differences in level—differences which may be very slight and therefore appear at first sight insignificant—can only be observed and recorded satisfactorily if the size, distribution and frequency of the units composing the mosaic have first been recognized and sampling methods adjusted accordingly. The recognition of the natural mosaic is, of course, often made more difficult by biotic interference.

The arrangement of soils and vegetation in the form of zones and mosaics, often of a detailed and complex nature, is a fact generally accepted by ecologists. Its manifestations in the field have, however, frequently been missed because of the use, especially in applied ecology, of unsuitable sampling methods—for instance, fixed intervals too widely spaced—without adequate preliminary reconnaissance or primary correlation of vegetation data with physiographic and soil data. It is in fact probable that a more consciously physiographic approach to the classification of both soils and vegetation, especially when extended to a detailed consideration of micro-relief, may assist the solution of many problems which have hitherto been the source of much confusion. Such an approach was, indeed, found indispensable to the understanding of the soil and vegetation types encountered in the Sudan. Although a good many African soil-vegetation systems of an

essentially similar kind have already been described from an ecological standpoint, interpretation in terms of catenas and mosaics of small units seems to be a novelty. A recent memoir by Roberty (1946) analyses the floristically similar vegetation of the Niger valley into smaller units than are usually recognized, but even so the absence of a catenary basis makes comparison of his units with our own almost impossible.

Within a defined region there are, of course, variants of the generalized catena, more or less distinctive according to the divergence in topography and rainfall which cause them. Recognition of these catena-variants is a further requirement in understanding the regional ecosystem. Actual instances are discussed later (p. 32). Amongst the catena-variants one might expect to find a type which, through a particular combination of nature of slopes and amount of rainfall, shows the clearest division of the main soil-vegetation units. Such a combination of conditions was found in the south-west Sudan close to Wau. Subsequent appreciation of the catena-variants has shown that this relatively clear representation of all three complexes of the catena in one place, displayed under the intermediate topographical and rainfall conditions close to Wau, simply reflects the fact that conditions more extreme in either direction (steeper and wetter, or flatter and drier) elaborate certain parts of the catena and suppress others.

Detailed studies made in this 'key' locality and in others farther afield are described in the last part of the paper. The data obtained are included in full in order to present a clear, factual picture of the soil-vegetation units whose recognition is essential if the catena/mosaic interpretation is to be successfully applied.

The concept of a composite or 'ideal' catena, for the whole of a defined topographic-climatic region, arose from a correlation of the detailed work with general observations made in other parts of the country. It has, indeed, become apparent that the catena/mosaic concept can be usefully employed in studying the soils and vegetation of most of the Anglo-Egyptian Sudan. Not only there, but also in similar country elsewhere, the concept, when applied in detail, can facilitate the recognition of the essential soil-vegetation status of any piece of ground and thus help in assessing potentialities of land for agriculture and forestry. There is, too, reason to believe that the concept can be even more generally applied in the study of soils and vegetation, though with varying degrees of advantage according to the conditions. Its closest application may be expected under conditions of climate and topography which give a decisive predominance to local differences in the role of water as a pedogenic and ecological factor, and where geologically caused soil differences are subordinate to those derived from water conditions.

EXPLANATION OF TERMS

Before proceeding further, the sense in which certain terms are used in this paper must be explained. Terminology for natural phenomena with gradations can never be rigidly fixed, and the following explanations are given merely in order to provide some standard for reference when the context leaves any obscurity.

Catena: A grouping of soil-vegetation types linked in their occurrence by conditions of topography and repeated in the same relationship to each other wherever the same conditions occur.† This relationship is most clearly seen where the component units are zonally arranged, and then the term catena is used to describe an observed zonal arrangement.

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† Modified from Milne (1935). Can be extended, as by Milne, to cover repeated geological, as well as topographical, conditions.

Mosaic: A soil-vegetation patchwork (in plan), usually following topography or microrelief. The units forming a mosaic may be of any size, shape or complexity, from unit catenas within a natural region† to phases within a complex (indeed, two illuvial phases, as at present classified, are themselves mosaic in pattern).

Complex: An aggregate of soil-vegetation units occupying one of the principal divisions of the main catena—either the top (eluvial complex), the slope (colluvial complex) or the bottom (illuvial complex).§ The arrangement of the units within a complex may be zonal or in the form of a mosaic.

Sub-catena: A term used for convenience to describe a complex (in the above sense) whose units are clearly arranged in a zonal manner.

Phase: The most closely defined soil-type unit which is distinct; related to others with which it forms a soil complex.||

Phase community: A discrete vegetational unit of the most closely defined order recognized; distinguished by floristic composition and co-extensive with a soil phase. The name or symbol of the soil phase is sometimes applied to its plant community for convenience.

Zone: A phase and/or phase community when occurring in a zonal manner (a complex composed of such zones being described by the term sub-catena given above).

It should be noticed that, among these terms, 'phase' refers to soil only, 'phase community' to vegetation only, and each of the others to soil or vegetation or (usually) both together.

Categories of soil-vegetation units

With the exception of 'mosaic', each of the foregoing terms is used for a unit or aggregation of a certain rank. For the terms given already, the ascending order in the hierarchy is: phase or zone; complex or sub-catena; catena. Expressed so as to cover soil and vegetation together, these categories may be summarized as follows, starting with the lowest:

Phasic unit: A soil phase with its phase community. Differing phasic units on the same main topographical site (top, slope or bottom) are grouped zonally or as a mosaic to form a

Complex: A given type of complex recurs throughout the natural region† on topographically corresponding sites, each observed example having the same relationships to the other types of complex near-by. A grouping of different types of complex constitutes a

Catena: Recurring as separate examples throughout the natural region under similar conditions of topography, disposed according to the topographical configuration and modified according to the modifications of topography and climate within the natural region. Repeated catenary manifestations together form the

Regional system: Conditioned by the climate and general type of topography of the natural region as a whole.

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† The natural regions are described below (p. 10).

§ There is no intention here to restrict the use of the convenient general term 'complex' to a unit of definite size or content. It has been used by Milne (1935) to refer to the whole 'catenary complex', as well as to a unit similar to our illuvial complex. The sense in which the word is used can be made clear by the addition of the relevant epithet.

|| In the case of the eluvial phases, which are distinguished largely by soil depth, the use of the term 'phase' follows its normal pedological meaning, but for the components of the colluvial and illuvial complexes—distinguished by texture and drainage rather than by depth—its use in the present paper involves an extension of the ordinary meaning.

II. GENERAL DESCRIPTION OF THE COUNTRY

The tract of country involved is the western and larger part of the province of Equatoria. It forms roughly a triangle, some 950 km. (600 miles) in its greatest extent, bounded on the north by the river Kir or Bahr el Arab, on the west and south by the frontiers of French Equatorial Africa, the Belgian Congo and Uganda, and on the east by the Bahr el Jebel, which is the upper portion of the White Nile. The travels of the expedition penetrated all the main parts of this area; the routes followed touched every place named on the map and also the Bahr el Arab north of Aweil.

The physiography of the area is dominated by the river system of tributaries flowing for the most part into the extensive Sudd swamp which surrounds the course of the Bahr el Ghazal and much of the Bahr el Jebel. As the map suggests, these tributaries from the south-west would make a very important contribution to the waters of the White Nile, were it not for the enormous wastage by evaporation from the swamps. A good description of the country and its rivers is given by Hurst & Phillips (1931).

With the exception of some scattered groups of abrupt rocky hills and mountains (jebels), mostly in the north-western and south-eastern corners of the region, the topography is on the whole gentle, very rarely abrupt, and takes the form of a peneplain whose dissections are the shallow river valleys following the gentle south-west to north-east slope of the 'plateau' from about 800 m. (2600 ft.) above sea-level along the Nile-Congo watershed, downward to about 400 m. (1300 ft.) in the Sudd region. The rainfall belts run roughly from west-north-west to east-south-east, across the line of the rivers and the general slope of the country, the total range of variation being from below 800 mm. (32 in.) annually in the north-east, to over 1500 mm. (60 in.) in parts of the southern border. (These and subsequent references to rainfall figures are from Hurst & Black, 1943.) The rainy season, varying in length according to region, occurs within the period March–November; August is generally the wettest month. In a given place the amount of rainfall and the duration of the wet season both vary considerably from year to year, especially in the northern and eastern parts of the region.

The soil problem is considerably simplified by a uniform underlying geological formation, the parent rock being nearly always basement gneiss. Blown sand occurs in some places along the northern border near the Bahr el Arab.

The natural vegetation over the majority of the area is savanna woodland (= tree-grass-woodland), that is to say woodland which, though its density varies, is never sufficiently dense or leafy to prevent dominance by grass in the herb layer. There is a marked admixture or even local dominance of thorny tree species in the drier parts of the north, and of broad-leaved deciduous or semi-evergreen† species in the south, but generally speaking the canopy species are small-leaved deciduous trees. The principal edaphic variants in the north-east and centre are thorn-savanna-woodland, thorn-scrub, flood-

† As used throughout this account, the terms 'semi-evergreen' and 'evergreen' indicate partial or complete retention, in a green and apparently functional condition through the dry season, of the foliage produced in the previous wet season or earlier. A few of the species classed as evergreen on this basis are true evergreens, retaining their leaves through two or more dry seasons. Some in both classes show variation from place to place and even from tree to tree. Under certain conditions, notably in high forest, it is admittedly difficult, without prolonged observation, to decide whether trees are evergreen or deciduous. The distinction as used here is, however, easily observed in savanna woodland areas, and there it is believed to be of definite value as an indication of the relative 'moisture-availability' of sites near together.
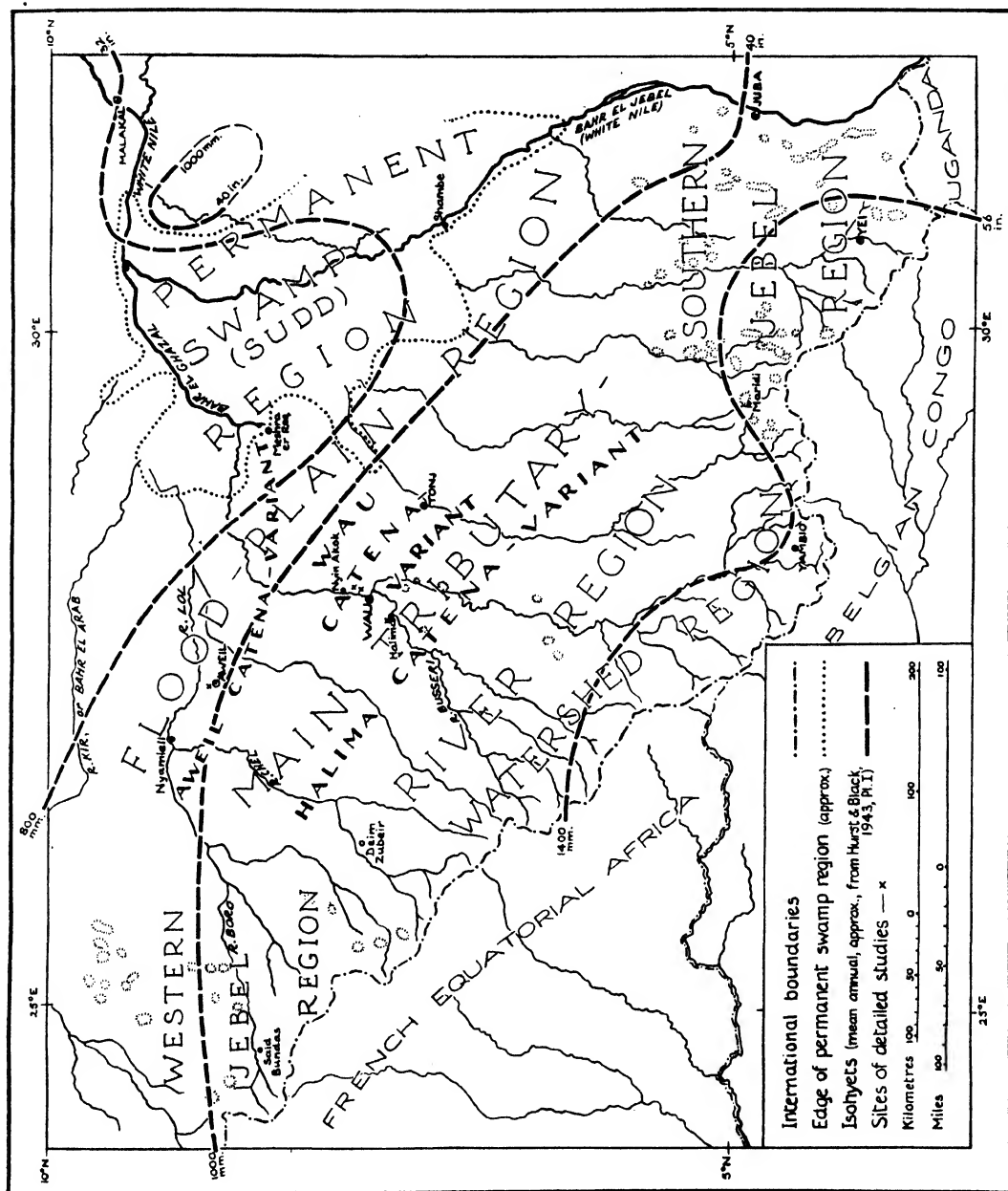
plain-grassland with or without scattered trees, and permanent swamp; in the south-west and south, gallery forest forms a closed evergreen canopy over the perennial streams.

NATURAL REGIONS

Within the major region studied, the natural divisions or regions are five, distinguished primarily by topography and rainfall. The general profile of the first four of these regions is shown diagrammatically in Fig. 1. Regions (3) and (4) are the main subject of the detailed descriptions following later.
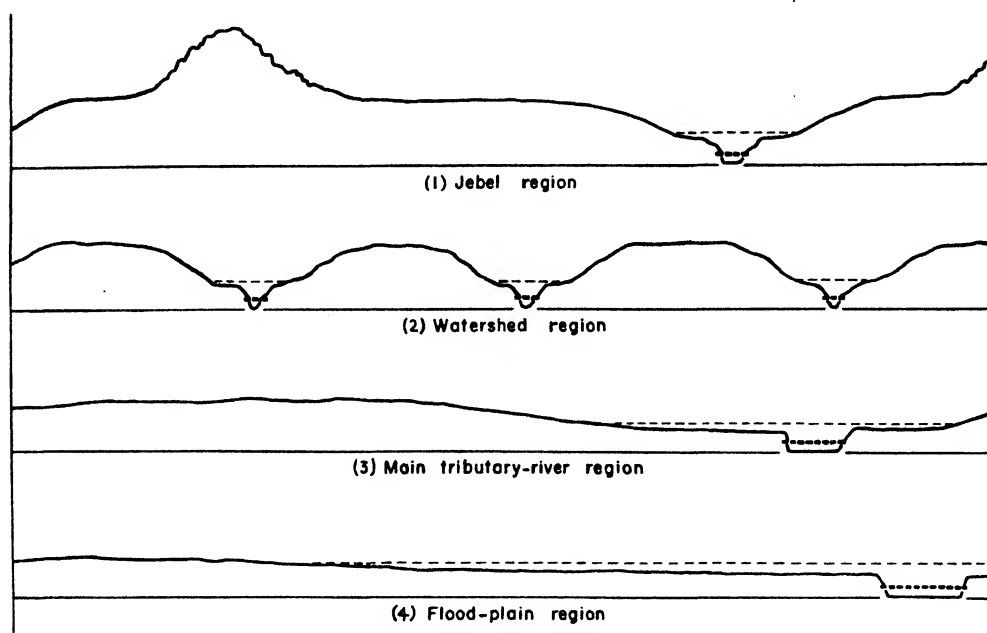
Fig. 1. General comparative profiles of the main natural regions. The almost flat permanent swamp region is omitted. The slopes and the relative river-widths are in all cases exaggerated. Water levels in relation to topography are shown thus:
– – – – – – wet season;   · · · · · · · dry season.

(1) *The jebel country* (Phot. 1) in the immediate neighbourhood of usually abrupt, rocky hills, is discontinuous, unimportant in extent, and was not examined in detail. Disregarding the features of the jebels themselves, two main characteristics of their immediate localities may be mentioned. The soils contain undecomposed rock-fragments, which are likely to provide a better supply of mineral nutrients than is available in the fully weathered eluvial soils elsewhere. Secondly, on the more or less flat ground near the foot of the jebels, where general appearances sometimes suggest a locally higher rainfall in addition to any influence of relatively good mineral nutrient supply, the savanna woodland includes species not seen on ground of similar character farther away from the hills. The chief jebel areas occur around the main source of the River Boro in the north-west, and in the Maridi-Yei-Juba district in the south-east. They form intrusions in, and share some of the characteristics of, the more extensive natural regions surrounding them.

(2) *The watershed region*, on and close to the low south-western watershed, and including the sources of the rivers, receives a fairly high rainfall, from 1250 mm. (50 in.)

Phot. 1. Typical jebel slope near the source of the R. Boro, in the western jebel region. Open, mixed, deciduous woodland including much *Burkea*, *Terminalia* sp. (*glaucescens* ?), *Combretum* spp. etc.

Phot. 2. A narrow valley in the watershed region, on the Congo border near Yambio. The cleared ground in front reveals the characteristic topography and a transverse view of the gallery forest with emergent *Khaya grandifoliola*.

Phot. 3. Mixed deciduous woodland on the higher ground at Yambio, in the watershed region. *Albizzia zygia, Acacia campylacantha, Ficus vallis-choudae, Anogeissus schimperi, Vitex doniana* etc.

Phot. 4. A typical subsidiary valley in the main tributary-river region near Wau. An extensive burnt area in the foreground (with mushroom-shaped termite mounds) permits a general view of the tree-dotted grassland in the valley bottom and of the denser woodland on the high ground beyond.

Phot. 5. Flood plain near Meshra er Req. Grassland mainly of *Hyparrhenia rufa*, with scattered trees and shrubs; *Sarcocephalus esculentus* in foreground.
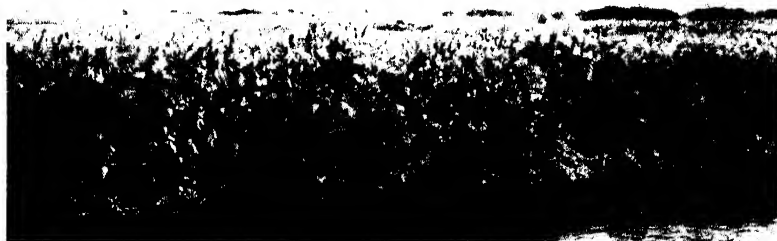
Phot. 6. Showing a stretch of slightly raised ground in the permanent swamp or Sudd region, bearing patches of *Acacia*. The riverside fringe is mostly *Cyperus papyrus*.
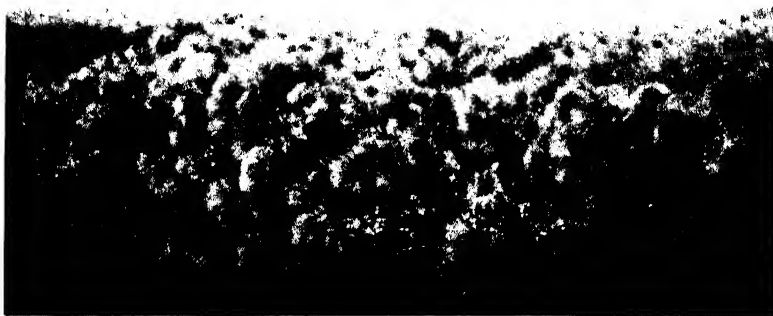
Phot. 7. Part of the permanent swamp between Malakal and Shambe, showing dominance by almost pure *Cyperus papyrus*.

to 1500 mm. (60 in.), distributed effectively over some nine or ten months of the year (February or March to November). Consequently the streams which form the head waters of the rivers are perennial; they are, too, fairly close together. The vegetation of the higher ground between the streams is dominated by large- and small-leaved deciduous trees forming closed or almost closed canopy, but with a fairly dense growth of tall grass beneath (Phot. 3). The narrowness of the valleys, and the great distance from the northern deserts with their desiccating winds, together produce a micro-climate in the valleys which, with perennial water, allows the growth in them of a far more luxuriant type of vegetation, the gallery forests (Phot. 2). Some species characteristic of gallery forest (e.g. *Chlorophora excelsa*) are occasionally found on the higher ground away from the streams.

(3) *The main tributary-river region* is the stretch of rolling country, traversed by the tributary rivers, between the watershed region and the flood-plains. The rainfall is lower than in region (2), varying from about 1000 mm. (40 in.) to 1250 mm. (50 in.) locally, and distributed over seven to eight months of the year (March or April to October). The smaller streams dry up completely in the rainless season. The shallow valleys of the rivers are comparatively wide (frequently several hundred metres across); they are separated by extensive stretches—often many kilometres—of relatively level or gently undulating higher ground (Phot. 4). The region as a whole is thus preponderantly one of eluvial and colluvial soils. The savanna woodland on the higher, well-drained ground is of a poorer and more open type than in region (2) (cf. Phots. 3, 8, 12 and 13). The gallery forest of the valleys dwindles progressively northwards to a mere river-bank fringe of evergreen trees of shorter stature and with leaves of a harder, smaller, more xero-morphic type. (Interesting evidence was, however, recorded by the late Dr J. G. Myers that well-developed gallery forest would extend farther north than it does but for the incidence of fires, whose severity increases with distance from the watershed.) The valleys, where level, are subjected annually to a fairly long period of flooding, and bear a characteristic valley grassland without trees, or in the better-drained parts with trees in varying density, but usually widely spaced, resembling an orchard (Phot. 11). These two latter types are virtually the same as the corresponding flood-plain types of region (4), but less extensive.

(4) *The flood-plain region* occupies the country traversed by the sluggish lower reaches of the main tributary rivers, and most but not all of it is flooded for part of the year. The wide, generally flat but sometimes uneven plains and their thinly timbered margins are inundated, like the valleys in region (3), partly by rain water direct, partly by local run-off from higher ground, but mostly by the flood water which spreads from the rivers in the course of the wet season. These plains are the main grazing grounds of the numerous cattle kept by the Nilotic Dinka people, whose villages are dotted on the stretches of slightly higher marginal ground, above the usual flood level. Rainfall here ranges from about 800 mm. (32 in.) to 1000 mm. (40 in.), falling during some six to eight months (April or May to October). The slightly raised ground which is free from floods bears what may be termed the normal woodland type, small-leaved, deciduous savanna woodland (Phots. 25, 28), often with a considerable admixture of thorny species. The major, seasonally flooded portion of the country is covered with a rather complex range of illuvial soils and corre-sponding 'low-level' plant communities. These are variants of open grassland (bearing the name 'toich' in the Dinka country); grassland with occasional trees and shrubs (Phot. 5) with gradations to very open savanna woodland (Phot. 35); light-canopied,

though sometimes almost closed, deciduous savanna woodland of characteristic type (Phot. 29); and the thorn-savanna-woodland of basin sites (Phot. 32); all being governed in their distribution by small differences of level and drainage. The orchard-like woodland mentioned under region (3) also occurs under similar conditions in region (4).

(5) *The permanent swamp or Sudd region* surrounds the Bahr el Ghazal and the lower reaches of the Bahr el Jebel, down to their confluence. Most of the ground is permanently waterlogged, including much that is permanently inundated. Slight differences in level are again reflected in the character of the vegetation (Phot. 6). Most of the permanently inundated parts are covered with enormous, more or less floating expanses of papyrus (*Cyperus papyrus*, Phot. 7), while the slightly higher ground supports grassland with or without trees and shrubs, similar to that of the flood-plain region shown in Phot. 5. The normal vegetation on relatively well drained sites in this region resembles that of the drier belts of region (4), ranging from mixed thorny and non-thorny woodland to pure thorn woodland of varying density.

Of the five natural regions, two were studied in some detail—the main tributary-river region and the flood-plain region. The remainder of this account refers to these only. They have to be considered jointly, since there is no sharp demarcation between them. The flood-plain region can indeed be described, in relation to the main tributary-river region, as that area where the illuvial complex, instead of forming relatively narrow bands, is so extensive as to qualify, with its associated tongues of higher ground, as a whole natural region.

III. MAIN TRIBUTARY-RIVER AND FLOOD-PLAIN REGIONS
FACTORS AND GENERAL CHARACTERISTICS

The principal climatic feature of both these regions is the marked contrast between the dry and wet seasons, with pronounced desiccation alternating with heavy rain and (in many places) floods. The very low humidity of the almost constant north-east wind during the five or six months of the dry season (November to March or April) plays a leading part in controlling the vegetation on well drained sites, while the floods, which eventually drain away and dry out on all but the lowest ground, control the low-level vegetation. The effect of these factors is accentuated or modified, to a degree difficult to assess, by yearly grass fires almost everywhere, and by shifting cultivation and erosion in many places. Soil and vegetation are naturally both powerfully affected, so that it is impossible to tell what the condition of the country would be in the absence of these disturbances. It must therefore be understood that what is being described is the soil and vegetation actually occurring under almost universal interference by one or more of these influences. Observations on fire-effects in woodland are discussed later (p. 56).

An additional factor of particular importance, especially within the rainfall range 800 mm. (32 in.) to about 1125 mm. (45 in.), is the apparently profound influence of termite activity on the soil, increasing depth, porosity, clay- and water-content, alkalinity (or decreasing acidity) and, as reported by workers elsewhere, concentrating bases (e.g. references by Thomas, 1943, p. 174). Termite mounds provide apparently damper habitats on high-level, well drained sites (Phot. 12), while in flooded localities they have the effect of raising islands of soil above flood level (Phot. 36). By these means, and on account of their abundance, termite mounds frequently affect the whole physiognomy of the

vegetation, while subterranean termite activities, though less spectacular, are much more widespread. Some preliminary studies of this question were made in the course of the investigation, but our knowledge of the manner in which termites are responsible for the development of soil and vegetation is still fragmentary. Although a beginning has been made in other parts of Africa, the need for detailed work is great and often receives comment in writings on tropical ecology.

From Table 13 (the only records from abundant termite mounds on the illuvial complex as well as from those on the higher levels) it appears that, within a locality, many species are characteristic of mounds both on the flooded and flood-free complexes, while other species seem to frequent mounds on one or other of these levels, but not both. A fuller study of this matter would no doubt be illuminating in connexion with the different properties mentioned above as possessed by eluvial-site and illuvial-site mounds—the former providing habitats damper than their surroundings in the dry season and the latter being flood-free islands in the wet season, but both possessing other characteristics in common. A careful analysis of the mound species in connexion with their occurrence away from mounds might likewise throw light on the ecology of a good many species. Such a study requires detailed local data from the various topographical levels and more extensive observations from other regions, as advocated by Michelmore (1934), who quotes relevant examples.

Termite mounds and their vegetation are further discussed in this account where they affect the interpretation of the data presented, in particular the observations made on a specific area of eluvial woodland (pp. 56–58). The species which appeared to be characteristic of termite mounds are marked with an asterisk in the Appendix (p. 81). The same sign is used for termite-mound species or occurrences in the various vegetation tables.

These factors of climate, flooding, fire, cultivation, erosion and termite action operate on a catenary system of which an outline description must be given at this stage.

In regard to soils, those of the eluvial complex are the shallowest, coarsest and most completely drained; those of the colluvial complex are in the main much deeper, finer and well drained; the flooded illuvial complex has the deepest soils, mostly of heavy texture, with drainage varying from fair (once it starts) to non-existent.

The vegetation of the eluvial complex is mixed savanna woodland (Phots. 8, 12, 13 and 14), rich in species and varying in detail, though not in fundamental character, according to local rainfall and depth of soil. The colluvial slope is dominated by comparatively few species belonging chiefly to a single genus (*Combretum*) of small trees or shrubs (Phot. 22). Such illuvial sites as are not altogether treeless grassland carry a still more restricted tree-flora usually dominated by one or other of six species—two of *Terminalia* (Phot. 11) and one each of *Pseudocedrela*, *Anogeissus* (Phot. 29), *Mitragyna* (Phot. 34) and *Acacia* (Phot. 32).

This distribution of species-dominance might be held to bear out the thesis that sites with free drainage, provided they are not unduly dry, carry the greatest number of species, while progressive interference with drainage reduces the number of species in favour of gregarious dominance by the few adapted to special conditions. But it must also be noticed that the fires, which are essentially grass- and not forest-fires, are most severe on the lower levels where moisture is sufficient to promote a dense growth of perennial grass. Sapling growth of woody species is thus more lightly scorched on the drier, upper levels, and the shading by trees and shrubs reacts to eliminate inflammable herbaceous growth

still further. The interaction of water conditions and fire as factors on higher and lower ground may be shown schematically thus:

Higher levels
↓
Ground drier

Wet season: Dry season:
No flooding   Little moisture at grass-root depth
↓   ↓
Trees encouraged —→ Shading —→ *Sparser grass*
↑   ↓
Saplings survive ←———————— Slight burning

Lower levels
↓
Ground wetter

Wet season: Dry season:
Flooding   Fair moisture at grass-root depth
↓   ↓
Trees discouraged —→ Little shading —→ *Denser grass*
↑   ↓
Saplings suffer ←———————— Severe burning
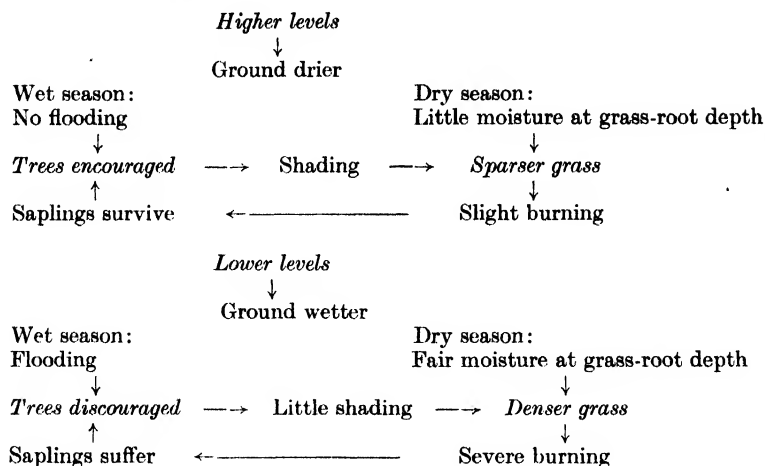
THE COMPOSITE CATENA

The soil-vegetation catena is illustrated in a much condensed form in Fig. 2. The following pages describe its soils and vegetation. Tables 1, 2 and 3 (pp. 17, 22 and 27) present summary descriptions and supplement the text with names of plants noted as characteristic of each soil phase.

These pictorial, descriptive and tabulated records of the catena are of necessity generalized. Moreover, the complete catena so recorded is a composite product. This statement is best explained in relation to Fig. 2, to which it applies with particular force. Here the representation of each complex is based on the catena-variant which displays it most clearly. Thus, speaking generally, the eluvial complex depicted is that of the variant seen just east of Wau, the colluvial is that seen at Halima and farther west and south, and the illuvial is that of the Aweil variant. Details shown by the transects studied at these places are freely modified, as necessary, from widespread observations of what was typical. The condensed drawing of the catena at the top of the figure naturally fails to give a realistic picture of the most extensive phases or zones; an obvious case in point is the treeless 'toich' (Il/Dr 2), which may be several kilometres across, or the *Terminalia* zone (Il/Dr 1), which is often greatly extended. An impression of the sort of area actually occupied by various phases may be gained from the photographs; some dimensions of particular samples are given in the last part of the paper (p. 34). The linear form imposed by a sectional view such as Fig. 2 necessitates certain sequences not strictly in accordance with observation. The Col/F 2 phase with its brake of bamboo was not observed, as depicted, in zonation between Col/F 1 (*Combretum*) and the Col-Il transition; nor was Il/Dr 1 seen to occur between Il/Id 2 and Il/Dr 2. The various illuvial soils and their conditions of occurrence are described in due course (p. 25); here it need only be explained that the impeded illuvials (Il/Id) occur characteristically where the lie of the ground hinders the flow of water to a drainage channel, and in enclosed valley-bottoms or depressions which have little or no outward drainage. They are therefore to be looked upon as alternatives to the drained illuvials (Il/Dr), rather than as occurring above or below them in a topographical sense, and Fig. 2 should be regarded with this in mind.

It should further be made absolutely clear that the descriptions which now follow present the whole composite catena in an entirety never seen in a single sequence, and with details of soil and vegetation compiled from extensive observation and not from any particular area.

SOIL AND VEGETATION TYPES

THE ELUVIAL COMPLEX

The greater part of the area of the high-level or E complex bears its soil phases in a mosaic pattern. They are known as 'ironstone' soils, from the almost universal presence of a compacted iron-accumulation (B 2) horizon† which, especially on exposure to air and desiccation, produces a red-brown, nodular, rock-like material of extreme hardness. The density and hardness of this horizon are usually in inverse proportion to the depth of the A horizon which ordinarily covers it. Whether the origin of the ironstone is to be sought in earlier geological ages or whether it is forming now is uncertain. Thomas (1946), writing of Uganda, adduces evidence that deposits of lateritic ironstone are there promoted by human settlement. In the south-western Sudan its occurrence seems far too universal and uncorrelated with population to be explained by such a hypothesis, although the movements of population which have occurred in the past make it difficult to draw immediate conclusions. It is possible, however, that while a climate optimal for the development of ironstone may have existed over much of the south-western Sudan, conditions in Uganda in this respect may have been marginal and therefore susceptible to the extra influence of human activity.

Whether the variation in the depth at which the ironstone is encountered may have been derived in the first instance from undulations in the underlying gneiss is a further conjectural matter. It is at any rate clear that its present depth below the surface affects the local development of the vegetation, which on the deeper soil patches forms a dense perennial cover and thereby reacts on the soil by protecting it from erosion. In many cases there is evidence that serious over-cultivation or severe and repeated burning has so impoverished the soil and the natural vegetation that erosion has removed part or the whole of the A horizon and in places even the layer of pea-iron§ concretions (B 1) underlying it. These phenomena are especially noticeable around the sites of previous Arab settlements, as in the neighbourhood of Wau and Tonj and the now deserted Arab towns of Deim Zubeir and Said Bundas farther west. Broad, treeless wastes, frequently in the form of slightly inclined 'erosion slopes', are a feature of the landscape near all these places (Phot. 4).

There is thus, within the eluvial complex, a mosaic or occasionally a zonation of soils among which the main effective difference is the depth of the A and B 1 horizons above the B 2 ironstone. These different soils constitute the various eluvial phases. The following have been distinguished:

Deep (E/Dp)	Shallow redistributed (E/S.R)
Deep + termite mound (E/Dp+)	Shallow eroded (E/S.Er)
Shallow (E/S)	(Ironstone) outcrop (E/O)

Eluvial-colluvial transition (E-Col)

† The symbols B 1 and B 2 are used for the upper and lower parts of the iron-accumulation horizon.

§ The useful term 'pea-iron', frequently employed in subsequent pages, describes the somewhat rounded concretionary granules of ironstone, with mean size about that of a pea, which occur either in bulk as a coarse gravel, or more sparsely, or singly.

A generalized summary of these soils and their vegetation is given in Table 1 (p. 17). The height and quality of vegetation on the various soil phases of the eluvial complex depend, as already implied, on soil-depth. Thus the tallest and most luxuriant vegetation, often including evergreen trees and shrubs, occurs on the E/Dp+ and E/Dp phases, and the lowest and most ephemeral, chiefly annual grasses and low herbs, on the E/S.R phase (Phots. 8, 12 and 13), while the bare ironstone of the E/O phase is unoccupied by plants, except for the cracks and pockets which really represent extensions or patches of deeper phases (Phot. 15). The incidence of fire is also largely dependent on soil-depth and vegetation. It often happens that the deeper phases escape regular burning, presumably because the grass remains green longer and is less dense owing to tree influence. Hence the difference between the phases tends to be accentuated by the fire factor.

On eluvial areas with appreciable slopes, the shallower phases can be seen to occur characteristically on the tops of the narrower ridges, at the edges of wider ridges, and on the upper parts of slopes. Some zonation of the phases then occurs. On more level eluvial areas, however, the six soil phases and their corresponding vegetation form a mosaic whose units appear haphazard in distribution, although the same governing factors of terrain no doubt apply in a less easily detected way. Large areas of eluvial ground are of this slightly undulating type. From the air they would show, especially after fire, a number of patches of E/Dp+ and E/Dp—the former of rounded shape, the latter larger and more diffuse—interspersed with rather more extensive and continuous areas and belts of E/S, E/S.R and E/S.Er, and limited patches and ridges of E/O, each recognizable by its vegetation or (E/O) the lack of it.

Termite mounds on the eluvial complex

While on the colluvial and illuvial complexes, later described, termite mounds occur on a variety of soil phases, the eluvial complex shows a virtual restriction of mounds (other than the small 'mushroom' type on E/S.R, which do not affect the vegetation appreciably) to the E/Dp sites. For this reason they are conveniently considered as a single phase, which is described below (p. 19) under the symbol E/Dp+.

Description of eluvial phases

Eluvial deep (E/Dp)

This soil phase, though somewhat variable in depth of A horizon (25–45 cm. = 10–18 in., rarely more) in different parts of the district, may be taken to represent the (apparently) uneroded soil of the deeper sites, perhaps in troughs or pockets in the micro-relief of the underlying rock. The A horizon is here deep enough to support a tree-cover sufficiently dense to prevent removal, through erosion, of the surface soil, which thus develops *in situ*. Where burning of the universal grass-cover is prevented, a light litter accumulates annually; it does not persist through the wet season because of the intense activity of the soil fauna, notably termites, and presumably because of the rapid bacterial decomposition characteristic of tropical soils. Normally, however, burning replaces the litter by a surface layer of ash which is washed into the soil.

The vegetation of this E/Dp phase is dominated by a mixture of small-leaved deciduous trees, many leguminous. With a rainfall of 1100 mm. (43 in.), as around Wau (Transect I), a variable proportion (up to 25% of individuals) of hard-leaved evergreen trees (*Khaya senegalensis, Daniellia oliveri,* etc.) is a characteristic feature (Phots. 8 and 12). With

Table 1. *Composite catena; soils and vegetation of the eluvial complex*

In the third column, species in each group (canopy trees, shrubs, etc.) are listed in approximate order of importance. The record of characteristic undershrubs, grasses and herbs is liable to be very incomplete.

Soil phase	Vegetation	Characteristic species
Eluvial deep E/Dp Relatively deep, uneroded phase of eluvial complex; A horizon of reddish, light-coloured soil over B1 pea-iron agglomerating below into B2 ironstone of varying hardness	Trees mostly deciduous; small percentage of evergreens or semi-evergreens. Canopy moderately open. Outstanding trees 15–18 m. (50–60 ft.) high; general canopy 9–15 m. (30–50 ft.) high; sub-dominant trees 4–6 m. (15–20 ft.) high. Shrubs and tall grass moderately dense	Principal canopy trees: *Prosopis africana* *Burkea africana* *Khaya senegalensis* *Daniellia oliveri* *Isoberlinia doka* *Parinari curatellifolia* *Sclerocarya birrea* *Albizzia sericocephala* *Afzelia africana* *Cordyla richardii* *Amblygonocarpus schweinfurthii* *Afrormosia laxiflora* *Erythrophleum africanum* *Manilkara schweinfurthii* *Detarium senegalense* Sub-canopy trees and large shrubs: *Crossopteryx febrifuga* *Hexalobus monopetalus* *Lonchocarpus laxiflorus* *Combretum lecananthum* *Strychnos innocua* *Gardenia lutea* *Oncoba spinosa*
E/Dp + Termite mounds built up on the E/Dp phase. Soil of variable colour and depth, of vesicular structure, containing a much higher percentage of clay than the E/Dp soil, and often palpably moist when the latter is dry	Trees evergreen and deciduous. Canopy dense, casting much shade, 12–20 m. (40–70 ft.) high. Sub-dominant trees and lianes, mostly evergreen, 4–9 m. (15–30 ft.) high, and shrubs, evergreen and deciduous, up to 2 m. (6 ft.) high, forming a dense thicket. Tall and short grass, very sparse. Various herbs	Principal canopy trees: *Khaya senegalensis* *Anogeissus schimperi* *Tamarindus indica* Lianes: *Hippocratea richardiana* *Opilia celtidifolia* *Landolphia* spp. Sub-canopy trees and large shrubs: *Maba abyssinica* *Diospyros mespiliformis* *Teclea nobilis* *Boscia salicifolia* *Ximenia americana* *Mystroxylon aethiopicum* Shrubs: *Popowia djurensis* *Rhus natalensis* Scramblers: *Adenia venenata* *Capparis corymbosa* Grass: *Beckeropsis uniseta* Herbs: *Sansevieria* sp. *Wissadula amplissima* var. *rostrata*
Eluvial shallow E/S Shallower, or partly eroded, phase of the eluvial complex, with a thin A horizon above the B1 pea-iron	Trees all deciduous. Canopy very open, 6–12 m. (20–40 ft.) high. Sub-dominant trees few and short. Deciduous shrubs 2–3 m. (6–8 ft.) high, rather dense. Medium-tall grass, usually very dense	Principal canopy trees: *Lannea schimperi* *Lannea kerstingii* *Terminalia mollis* Small trees and large shrubs: *Crossopteryx febrifuga* *Combretum ghasalense* *Strychnos spinosa* *Combretum verticillatum*

Table 1 (*continued*)

Soil phase	Vegetation	Characteristic species
Eluvial shallow redistributed E/S.R Shallower than E/S; A horizon apparently mixed with ash and redistributed	Occasionally a few shrubs, but usually only a dense growth of annual grasses and herbs 45–60 cm. (1½–2 ft.) high, with or without a variable mixture of undershrubs, perennial herbs (some bulbous) and tufts of perennial grass	Trees: None Shrubs: *Gardenia* sp., usually *G. triacantha* Undershrubs: *Lepidagathis* sp. aff. *fischeri* *Barleria grandicalyx* Grasses (annual): *Ctenium elegans* *Hyparrhenia barteri* var. *calvescens* Herb: *Urginea indica*
Eluvial shallow eroded E/S.Er No A horizon; B1 pea-iron on the surface	Small trees and shrubs, deciduous, often forming a fairly dense thicket, 2–4·5 m. (6–15 ft.) high. Medium-tall grass, about 1·3 m. (4 ft.) high, probably fairly dense with annual species before burning	Large trees: None Small trees and shrubs: *Hymenocardia acida* *Combretum verticillatum* *Bridelia scleroneuroides* *Grewia mollis* *Gardenia* sp., usually *G. triacantha* Grasses: *Ctenium elegans* *Hyparrhenia barteri* var. *calvescens* *Sporobolus* sp. (*festivus* ?)
Eluvial (ironstone) outcrop E/O Exposed ironstone of the B2 horizon, or ironstone formed on parent rock	No vegetation at all except in cracks in the ironstone, and in occasional pockets, *which are not part of the phase proper*. Trees, shrubs, undershrubs, perennial and annual grasses and herbs occur in varying proportion in such places	Vegetation of cracks and pockets of varying depth: Trees: *Diospyros mespiliformis* *Manilkara schweinfurthii* Undershrubs: *Indigofera bracteolata* *Lepidagathis* sp. aff. *fischeri* Grasses (annual): *Ctenium elegans* *Hyparrhenia barteri* var. *calvescens*
E-Col Transition between eluvial and colluvial, occurring where sufficient slope and rapidity of erosion have led to the accumulation of an appreciable quantity of ironstone blocks and fragments	Usually a dense grove of evergreen and/or broad-leaved deciduous trees, often with lianes, and with evergreen small trees and shrubs beneath; all these growing in pockets between ironstone blocks; little grass	Principal canopy trees: *Khaya senegalensis* *Manilkara schweinfurthii* *Diospyros mespiliformis* *Isoberlinia doka* *Afzelia africana* Sub-canopy small trees and large shrubs: *Diospyros mespiliformis* *Maba abyssinica* *Teclea nobilis* Lianes: *Hippocratea richardiana* *Opilia celtidifolia* *Landolphia* spp. Shrubs: *Popowia djurensis* *Rhus natalensis*

about 1000 mm. (40 in.) rainfall (around Aweil, Transect III) this proportion is much less (Phot. 25). Above 1125 mm. (45 in.) rainfall, broad-leaved deciduous trees (especially *Isoberlinia doka*) tend to become dominant (Phot. 14). The general height of the canopy varies from 9 to 15 m. (30–50 ft.) according to rainfall, with outstanding trees attaining 15–18 m. (50–60 ft.). The understory, mostly deciduous shrubs and small trees 1·5–6 m. (5–20 ft.) high, varies in density according to the amount of shade and the fierceness and frequency of grass-fires, and partly consists of saplings and coppice (regrowth from burnt or cut stumps) of the canopy species. The herb layer is dominated by tall, mostly perennial grasses about 1·5 m. (5 ft.) high, and herbs of which little remains in the dry season. The

amount of shade cast by the canopy, which is mainly deciduous, is difficult to assess, but in practice it is insufficient to shade out the grass, which only becomes sparse immediately beneath spreading evergreen trees.

Termite mounds on E/Dp sites (E/Dp+)

The distinctive and interesting phase which originates from termite building on the eluvial complex is nearly always found on areas of E/Dp, as reflected by its symbol E/Dp+. Termite mounds, often large, are built up on the surface and subsequently collapse gradually. Whether inhabited or derelict, they greatly increase the depth of soil available to plant roots. In the dry season, moreover, the soil of the mounds is appreciably damper to the touch than that of the surrounding E/Dp, and usually its reaction is markedly less acid. These conditions make possible, on and immediately around occupied or abandoned mounds, the continued existence of small patches of a more luxuriant type of vegetation. It is not known whether the whole of this vegetation has been able to establish itself there only after the arrival of termites, or whether the termites concerned would build mounds except under fairly dense shade; newly built mounds were certainly not observed in the open on E sites.

The E/Dp+ phase is therefore very important in that it supports islands of evergreen vegetation in the midst of the largely deciduous tree population on the E/Dp phase (Phot. 12). Small patches of E/Dp, surmounted by a termite mound, often occur isolated in stretches of E/S or E/S.R. Each termite-mound plant community is usually dominated by one or more large individuals of evergreen *Khaya senegalensis* 15–20 m. (50–70 ft.) high, usually associated with the deciduous *Anogeissus schimperi*. A special association of evergreen small trees like *Maba abyssinica* (Phot. 13) and *Diospyros mespiliformis*, with shrubs and saplings, forms a dense, often almost impenetrable understory, sometimes with the addition of scramblers and lianes reaching the tops of the smaller trees. These small islands of evergreens, usually only a few metres across, are not penetrated by fires which burn through the surrounding area. This is because growth of grass beneath them is prevented by the heavy shade, which is also responsible for a sparser growth of grass immediately around each island than farther away. What grass there is close at hand remains green until after the usual firing-time through the influence of shade and the higher water-content of the mounds. These protected islands of vegetation can act as a continual source of seed, which may lead to regeneration on the surrounding E/Dp and E/S phases if burning is prevented (p. 58).

Eluvial shallow (E/S)

The E/S phase comprises those parts of the complex where the A horizon is less deep. Whether this is due to originally shallower soil or to erosion hardly affects the result, which inevitably means less soil-depth and moisture available to plant roots during criticial periods. The tree vegetation is decidedly more deciduous and open than on the E/Dp phase. Its appearance and height with about 1100 mm. (43 in.) rainfall are similar to those seen on the E/Dp phase in areas where the rainfall is only 875–1000 mm. (35–40 in.). Compared with examples of the E/Dp phase in the same neighbourhood, the trees are fewer, shorter and more spreading, two species of *Lannea* and one of *Terminalia* being especially frequent; the shrub layer is denser and plays a more important part, and the grasses and herbs are more numerous in species and much denser (Phot. 8). The pro-

portion of highly fire-resistant trees and shrubs is also greater, which is natural enough, since the E/S vegetation as a whole is more inflammable than that of E/Dp.

Eluvial shallow redistributed (E/S.R)

The origin of this phase is inferred to be the shallower variants of E/S when exposed, after burning of the grass, to the full effect of heavy rains. The shallow A horizon is mixed with its surface deposit of ash and probably shifted from place to place (redistributed, R) by a creeping flood. A characteristic feature of this phase, at about 1100 mm. (43 in.) rainfall, is a type of small, mushroom-shaped termite mound about 30 cm. (1 ft.) high (Phots. 4, 12). The phase often occurs on long, very gentle slopes, and here it apparently represents eroded material on the move towards its sorting out on the colluvial slope below. This removal of surface material presumably results in the completely eroded phase E/O. Deeper pockets of soil which do not strictly belong to this phase may support a few trees and shrubs, but the characteristic E/S.R vegetation is a mixture of annual grasses 45–60 cm. (1½–2 ft.) high (*Ctenium elegans, Hyparrhenia barteri* var. *calvescens*) with or without scattered tufts of taller perennial grass, bulbous and other herbs, and undershrubs (Phot. 13). The last-named, though woody, often behave as perennial herbs, shooting freshly from the base each season.

Eluvial shallow eroded (E/S.Er)

It seems evident that this phase, whose surface is largely composed of pea-iron, has been derived, by removal of the A horizon, from E/Dp and E/S; the latter is peculiarly susceptible to erosion after burning, especially where the slope is appreciable. This E/S.Er phase is relatively rare except in the western and to some extent in the southern parts of the country examined, where the slopes are steeper. It bears less perennial grass than E/S, but its growth of annual grass, as indicated by ash seen after burning, may be considerable. Although it has no A horizon in the usual sense, it supports a fairly dense growth of shrubs 2–4·5 m. (6–15 ft.) high, the characteristic species being *Hymenocardia acida*, conspicuous because of its pale, pinkish grey or buff-coloured bark (Phot. 19). Coarser soils like this seem to favour the growth of xerophytic shrubs rather than grass. The species of such shrubs are few and very regular in their occurrence.

Eluvial (ironstone) outcrop (E/O)

This phase, consisting only of the hard, inhospitable ironstone (Phot. 15), is presumably the final result of erosion, or may perhaps sometimes result from the formation of ironstone on the surface of exposed parent rock. It carries no vegetation at all except in cracks and pockets, where occasional shrubs and undershrubs and even evergreen trees (notably *Manilkara schweinfurthii*) gain a foothold. The heath-like *Indigofera bracteolata* is frequent in such positions where they occur under a rainfall of about 1100 mm. (43 in.).

Eluvial-colluvial transition (E-Col)

Where topography is sufficiently abrupt and erosion has been sufficiently rapid, an accumulation of ironstone detritus is found at and below the edges of the E mosaic. By reason of its power of holding up eroded soil to form locally deeper pockets, this transition zone normally bears a more luxuriant tree growth than does the E/Dp phase, including a higher proportion of evergreens or of more mesophytic, broad-leaved deciduous trees.

Thus a rather dense grove of *Khaya, Diospyros* and/or *Manilkara*, with associated ever-green shrubs, often occurs here, and *Isoberlinia doka* seems to favour such a site at the drier, north-eastward limit of its range (apparently a little north and west of Wau).

This transition zone is not represented in Fig. 2, illustrating the composite catena, since the gentle type of relief there shown does not promote its occurrence.

THE COLLUVIAL COMPLEX (SUB-CATENA)

On the slope from the high ground there is a gradation of the material derived from the eroded parts near the edge of the eluvial complex. The material consists of the A horizon and often some of the loose B1 pea-iron gravel. This is sorted out, on its way down the slope, so that the coarsest material, including ironstone fragments or pea-iron, comes to rest in the highest zone, while the finer fractions are carried farther down the slope. With them some coarser material may also be carried, as evidenced by the worn pea-iron particles which are often found to a fair depth in lower zones; but they are quite insufficient to confer a gravelly character on the lower colluvial soils. Differences in soil here depend mainly on particle size and not, as in the eluvial complex, on differences in depth of an A horizon. The soils, though more weathered than the eluvials, are less mature in profile development. Whereas the eluvial complex, or nearly all of it, consists of an apparently random mosaic, the colluvial complex consists of a zoned sub-catena varying from coarse-grained, shallow soils at the top to fine-grained, deep ones at the bottom. The resulting marked differences of texture make it impossible to regard these soils as type-variants of a single series, and it is therefore proposed to regard them as distinct components which together make up the colluvial complex. For purposes of classification they have been divided primarily into coarse and fine colluvials. This distinction is based on general observation rather than soil analysis, which takes no account of pea-iron. The following colluvial zones have been recognized:

Coarse (Col/C)
Fine 1 (Col/F1)
Fine 2 (Col/F2)
Colluvial-illuvial transition (Col-Il)

Table 2 (p. 22) summarizes the characteristics of these zones.

Termite mounds on the colluvial complex

The termite mounds (Col/C+, Col/F1+, Col/Il+) on the colluvial and Col-Il soils are infrequent and do not appear to bear any plant species characteristic of them as con-trasted with termite mounds on the eluvial and illuvial complexes. Their flora is a mixture of species typical of the E/Dp and E/Dp+ phases with others characteristic of the termite mounds on lower sites such as Il/Id1+ and Il/Id2+. On the colluvial and Col-Il zones, as well as on the eluvial complex, termite mounds are often spread out by native cultivators to improve the surrounding soil, and local alteration in the physical and chemical composition of the soil may result (cf. pp. 52, 69).

Description of colluvial zones

Colluvial coarse (Col/C)

The soil here, although it retains some fine material, is very coarse-grained. The zone is never wide and occurs only where the slope is steep enough, and the rainfall sufficient, to move the larger soil particles. Hence it was not observed in Transect III, on the

Table 2. *Composite catena; soils and vegetation of the colluvial sub-catena*

In the third column, species in each group (canopy trees, shrubs, etc.) are listed in approximate order of importance. The record of characteristic undershrubs, grasses and herbs is liable to be very incomplete.

Soil phase	Vegetation	Characteristic species
Colluvial coarse Col/C Coarser, shallower, upper zone of the re-sorted colluvial material; light-coloured, reddish or pinkish soil	Trees few, deciduous, 6–9 m. (20–30 ft.) high. Canopy very open. Shrubs, often sparse. Tall perennial grass, usually rather dense	Canopy tree: *Butyrospermum parkii* var. *niloticum* Shrub: *Hymenocardia acida*
	Col/C+ (Not examined. No large termite mounds observed on Col/C)	
Colluvial fine 1 Col/F 1 (By far the most extensive of the colluvial zones.) Finer, deeper, lower zone of the re-sorted colluvial material; light-coloured, reddish soil	Small trees (*Combretum* spp.), deciduous but leafing in the middle of the dry season, up to 7·5 m. (25 ft.) high. Shrubs; coppice from burnt stumps. Rarely outstanding trees up to 20 m. (70 ft.) high. Tall perennial grass, dense, with herbs and undershrubs	Large trees: Rare individuals of *Daniellia oliveri* *Khaya senegalensis* *Pterocarpus abyssinicus* Small trees and shrubs: *Combretum undulatum* *Combretum glutinosum* *Combretum verticillatum* Other *Combretum* spp. *Acacia seyal* var. *multijuga* Undershrubs: *Cochlospermum tinctorium* *Lepidagathis appendiculata* Grasses: *Hyparrhenia rufa* and/or *Andropogon gayanus*
Col/F 1+ (Soil not examined. Large termite mounds rare on Col/F 1)	A mixture of trees and shrubs in groups of varying density, forming occasional evergreen islands in the Col/F 1 vegetation	No characteristic species; usually a mixture of E/Dp+ species and others
Colluvial fine 2 Col/F 2 Lowest colluvial zone with finest of the re-sorted material, occurring only under special conditions of topography; dark-coloured, chocolate brown soil	Dominated by numerous clumps of bamboo, with woody stems to at least 5 cm. (2 in.) diameter at the base, and some 9 m. (30 ft.) high. Sometimes also a few trees and shrubs characteristic of the zones above and below this, their presence depending on the density of the bamboo. Tall perennial grass, moderately dense. A special type only observed in association with the Halima catena-variant (see p. 24)	Dominant of tree/shrub layer: *Oxytenanthera abyssinica*
Col-Il Transition between Col/F 1 and Il/Dr 1 or Il/Id 1, in the absence of Col/F 2. Soil grey-buff, often with rather large, reddish sand grains on its smooth surface	Trees deciduous, except for occasional evergreens on termite mounds (Col-Il+). Canopy very open. Exceptionally tall perennial grass up to 3 m. (10 ft.) high. A widespread variant consists of groves and single trees standing in cultivated ground (see p. 25)	Locally dominant trees: *Entada sudanica* *Acacia hebecladoides* Subsidiary trees and shrubs: *Acacia seyal* var. *multijuga* *Gymnosporia senegalensis*
Col-Il+ (Soil not examined.) Termite mounds built up on the Col/Il transition	Groups of evergreen and deciduous trees and shrubs on the frequent termite mounds are a characteristic feature on Col/Il sites	No characteristic species; usually a mixture of E/Dp+ and Il/Id 2+ species (see Tables 1 and 3, pp. 17 and 27)
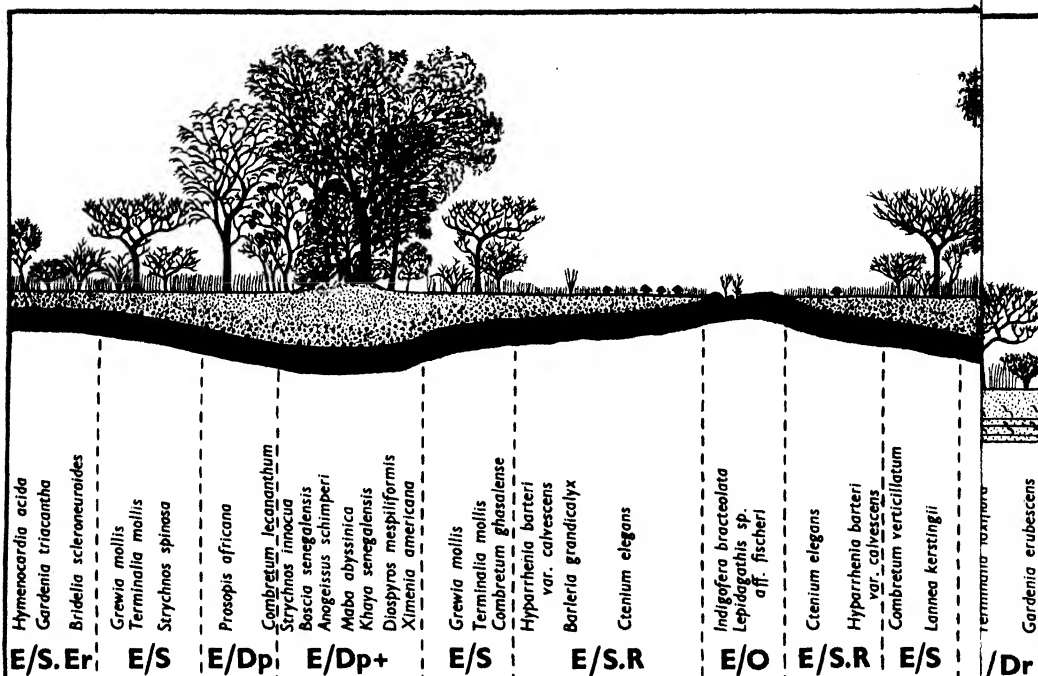
Savanna woodland, scrub, and short grass; great variation

"High-level" ironstone

ELUVIAL (E) COMPLEX
(usually mosaic)

Soil phases differing in depth of A horizon over B1 pea-i

Species labels (left to right, vertical):
- Hymenocardia acida
- Gardenia triacantha
- Bridelia scleroneuroides
- Grewia mollis
- Terminalia mollis
- Strychnos spinosa
- Prosopis africana
- Combretum lecananthum
- Strychnos innocua
- Boscia senegalensis
- Angeissus schimperi
- Maba abyssinica
- Khaya senegalensis
- Diospyros mespiliformis
- Ximenia americana
- Grewia mollis
- Terminalia mollis
- Combretum ghasalense
- Hyparrhenia barteri var. calvescens
- Barleria grandicalyx
- Ctenium elegans
- Indigofera bracteolata
- Lepidagathis sp. aff. fischeri
- Ctenium elegans
- Hyparrhenia barteri var. calvescens
- Combretum verticillatum
- Lannea kerstingii
- Gardenia erubescens

Zone codes: E/S.Er | E/S | E/Dp | E/Dp+ | E/S | E/S.R | E/O | E/S.R | E/S | /Dr

Eluvial shallow E/S	E/Dp+ (Termite mound on E/Dp site)	Eluvial shallow redistributed E/S.R	Eluvial outcrop E/O
reddish sandy loam and pea-iron		sandy loam and pea-iron mixed	
hard ironstone		hard ironstone	bare, hard ironstone
		(mushroom-shaped termite mounds common)	

Soil depth in cm.
0 –
15 –
30 –
45 –
60 –
75 –
90 –

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extremely gentle topography of the Aweil neighbourhood, but it was conspicuous on the steeper Transect II at Halima (Ngowlima) and in many places farther west. A layer of moderately hard concretionary ironstone usually underlies a mixture of soil and pea-iron. The vegetation of this upper zone is characterized by trees of *Butyrospermum parkii* var. *niloticum* (Phots. 20, 21), with or without a thicket of *Hymenocardia acida*. This last-named shrub or small tree seems to be typical of coarse-grained, shallow soils, notably the E/S.Er phase of the E mosaic, where pea-iron forms the dominant fraction of the surface soil. *Butyrospermum* is found scattered (though less well grown than on Col/C) on the E/S phase in the Wau district (Transect I) and also occurs in parts of the ill-defined colluvial zones at Aweil (Transect III, sections IV and V). There is therefore little practical difference, under the conditions observed, between shallow, eroded eluvial phases, and the coarser grades of the material eroded from them, as is natural enough.

Two 'fine colluvial' phases (zones) were observed in the present investigation. The upper of these (Col/F 1) occurred regularly; the lower (Col/F 2) was a special type.

Colluvial fine 1 *(Col/F* 1)   .

This deep soil consists of fine-grained, reddish, uniform material showing little horizon-differentiation until a horizon is reached containing a considerable quantity of concre-tionary 'ironstone' which is not hard until it has been exposed to the air by digging. Apart from the rare and inadequately understood occurrences of Col/F 2, the soil repre-sents the finest-grained product of colluvial re-sorting. It is essentially a moist soil, and still remains so when the soils of the E mosaic are dry. In the Wau district nearly all cultivation takes place in the Col/F 1 zone, except the 'low-level' cultivation of the Dinka tribe who live on the margin of the toiches (flood-plain grasslands), and the 'high-level' cultivation of old termite mounds on the E soils by the Jur tribe who inhabit the iron-stone woodlands. There is no doubt that under the rainfall of this district the Col/F 1 soil is much more productive agriculturally than those of the E mosaic.

The vegetation of the Col/F 1 zone is conspicuous and characteristic, being always dominated, under the conditions at present prevailing, by species of *Combretum* (Phot. 22). Owing to the strong tendency of dry-country species of this genus to break into new leaf in the middle of the dry season, the zone at this time appears from a distance as a bank of fresh green in a landscape of reddish brown and yellow tints. The presence in some places of single large trees of *Daniellia oliveri* and *Khaya senegalensis*, left standing by cultivators, suggests that in the absence of interference this zone should bear woodland of good quality. Even where there is no visible evidence of interference by previous cultivation, however, the dominance by *Combretum* species, as small trees, is undiminished, so that fire-selection would appear responsible for the absence of a better woodland type. The comparatively moist soil of the zone encourages a grass and herb layer which is both dense and tall and burns very fiercely and rather late. Probably few tree saplings are able to withstand such fires, while the Combretums quickly throw up vigorous coppice shoots after burning and therefore possess an advantage. It seems, however, that their dominance is not merely due to fire-resistance, for the particular species of *Combretum* most characteristic of this zone are rare on, or absent from, other soils in the same district, even under similar fire conditions. Apart from these Combretums, the zone under existing conditions is poor in characteristic species, and since it is the principal component

of the colluvial complex, the latter as a whole shows the same poverty. This may be judged from Table 4 (p. 35).

Colluvial fine 2 (Col/F2)

This very distinctive zone was observed only at Halima and in other places where topography and drainage conditions seemed to be of a similar character, and where there was neither a Col-Il transition zone nor a well-developed illuvial complex. It seems likely that the vegetation (bamboo brake) of the Col/F2 zone is associated with relatively immature colluvial soils derived in part from the direct erosion of parent gneiss, as well as from ironstone. This view is supported by the frequent and characteristic occurrence of bamboo in pockets of soil on gneiss jebels, and on ground in their immediate neighbourhood. Special water conditions may also be involved. The soil, rendered most distinctive by its chocolate brown colour, is a rather heavy loam, but loose and friable down to about 20 cm. (8 in.); below this there is a horizon showing clod-structure and some iron staining, but no sign of developing ironstone was seen.

The vegetation consists chiefly of numerous clumps of the bamboo *Oxytenanthera abyssinica* (Phot. 23), with woody stems attaining at least 5 cm. (2 in.) in diameter at the base and 9 m. (30 ft.) or more in height. Where the bamboo is not too dense, there are a few trees and shrubs otherwise characteristic of the zones above and below, and a moderately dense growth of tall perennial grass.

Colluvial-illuvial transition (Col-Il)

At the lower edge of the Col/F1 zone, where it grades into the low-level, illuvial (Il) complex, there is a zone transitional in soil character as well as in position. When bare the soil presents a smooth, washed appearance on the surface. The bulk of it is greyish or buff instead of red, although it often carries a superficial scatter of rather large reddish sand-grains. This transition zone is probably the meeting place of the downwash from above and the flood which rises from lower ground and whose margin occupies varying positions during the wet season. It is wider, and may become complex, where the topography is relatively flat.

It is doubtful if any but secondary vegetation was observed on this zone. It is too variable and often too open to display any regular woody association, but *Entada sudanica* seems to be a characteristic tree, in so far as there is one (Phots. 27, 28). When relatively undisturbed, the zone bears a particularly tall growth of perennial grass up to 3 m. (10 ft.) high. At least in the Wau district the Col-Il transition is usually marked by a row (when the zone is narrow) of rather large, grey termite mounds with a few evergreen and deciduous tree- and shrub-species found in other zones.

As far as can be ascertained, the Col-Il transition zone, or at least a zone occupying the same topographical position relative to the flooded low-level ground, is the one chiefly used by the widespread Dinka and other Nilotic tribes for their cultivation. Large, plain-like areas, sometimes several kilometres in extent, lying just above flood-level and carrying scattered villages, occur throughout the flood-plain region and the transitional belt between it and the main tributary-river region, for instance between Aweil and Meshra er Req. The natural vegetation seems to have been replaced by open park-like country with scattered large trees and large and small groves resembling orchards. Because most of the inhabitants live on such areas, and many roads pass through them, this unnatural but

very extensive type of vegetation becomes associated in the mind of the traveller with this part of the Sudan.

The most characteristic species are *Borassus aethiopum* (doleib palm), occurring singly and in extensive groves, *Acacia albida*, occurring singly or a few together, and *Ficus platyphylla* and other figs, usually occurring singly as very large, spreading trees. In places, especially in the flood-plain region, *Balanites aegyptiaca* (heglig) is locally frequent. *Kigelia aethiopica* and *Parkia oliveri* also seem to be favoured by the conditions and often grow to a large size. *Borassus*, because of its distinctive and striking appearance, is the most conspicuously regular in its occurrence. *Acacia albida* is rarely if ever seen far from villages. All these trees are left standing by the inhabitants, or sometimes are planted, as sources of food or shade.

THE ILLUVIAL COMPLEX

Below the colluvial sub-catena there is a complex of low-level, periodically flooded soils. One source of the flood water is downwash from the neighbouring slopes; usually there is also a more general, valley or plain flood. Considerable quantities of dissolved and suspended matter are brought by these means. The water arrives after more or less rapid movement and then drains away slowly or stands and evaporates, and the result (in contrast to that on colluvial sites) is the permanent retention of much or all of the fine, water-borne material.† Colluvial material (from adjacent slopes) preponderates in some of the soils, notably certain minor valleys and small basin sites (both 'low-level' only in relation to their immediate surroundings and often not subject to a general flood); alluvial material (from a distance) preponderates in others, notably in those on the broad, grass toiches; but common to all are the two features: a gain of fine, water-borne material,† and seasonal flooding.

The depth, duration and behaviour of the flood, whatever its origin, vary according to site and depend on general topography, distance from rivers or subsidiary drainage channels, and micro-relief. Thus there are, within low-level areas, riverain sites, from which water is lost mainly by drainage, and sites with little or no drainage, from which water is lost mainly by evaporation. Again, parts of a site may be surface-flooded only intermittently or only in years of high flood, but the development of their soil is affected by the longer persistence of the flood on adjacent parts. The variation in soil is therefore considerable, and the complexity is greatest where the general slope is very slight; here micro-relief has its maximum influence, as in the flood-plain region represented by Transect III (p. 67). The different soils and the vegetation on them occur either as a sub-catena of zones where the gentle slope is continuous, or as a mosaic where there are local elevations and depressions in a very gentle, general slope.

Although minor variations are innumerable, the low-level soils may be divided into two main types, drained illuvials (Il/Dr) and impeded illuvials (Il/Id), differing in kind of drainage, and each of these may be subdivided according to the depth and duration of flooding or the degree of impedance.

The illuvial drained (Il/Dr) soil sites are riverain in character in that there is evidently nothing to prevent the prompt movement of flood water towards a drainage channel as soon as the latter's water-level falls. In addition, the flood probably moves, albeit slowly, throughout the wet season. Conditions which are riverain in this sense often obtain even when the channel is a river 2–3 km. (1–2 miles) or more distant; they are not to be con-

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† This statement is qualified in the case of Il/Dr 1 soils (p. 29).

fused with riparian, or river-bank, conditions. On these 'drained' sites the surface of the ground is even, i.e. devoid of undulations, though usually sloping very gently. The conditions of terrain which produce free drainage are those which produce zonation rather than mosaics, and the Il/Dr phases are therefore nearly always zoned. Two phases of this drained type were clearly recognized. These are styled Il/Dr 1 and Il/Dr 2, the second being topographically lower (often a difference in level of inches only) and therefore flooded for a longer period and to a greater depth. In all probability more subdivisions could be distinguished; in fact, general observations strongly suggest that such exist.

The illuvial impeded (Il/Id) soil-sites have in common a kind of drainage fundamentally different from the 'drained' type in that the surface of the ground is uneven or concave; the extreme case is a basin site with no drainage at all. The uneven surface results in a prevalence of mosaics of phases instead of or as well as zones. Although the depth of flooding may be no greater (it is often less) than in the drained types, there is interference with the departure of the flood, and while it remains it is of a stagnant nature. Consequently the soil horizon showing iron mottling due to imperfect aeration is thicker and occurs nearer to the surface. The greater the impedance, the higher is the proportion of water evaporated instead of drained away; the greater is the clay content, resulting, when the soil dries, in cracks which may be deep; and the darker is the colour of the lower soil horizons until finally, in the completely undrained basin site, the whole soil is uniformly dark grey or black, except where it includes calcium carbonate concretions. (These, incidentally, also occur quite often on slight elevations in the impeded phases.) It is well known that this progressively darker colour, as compared with the red of typical 'red-earths' occupying higher levels in the catena, is no sure indication of more humus or less iron, but results from reduction of ferric to ferrous iron under stagnant conditions (Vageler, 1933, pp. 53–4).

Whether illuvial drained or illuvial impeded soils occupy the level immediately below the colluvial (or colluvial-illuvial transition) depends therefore on the drainage conditions induced by the local surface topography on the scale of macro- or micro-relief, or by the no less important subterranean topography of such impervious layers as may exist. The surface doubtless often expresses the micro-relief of such underlying layers, but may sometimes bear no relation to it.

The illuvial soils, with their vegetation, are summarized in Table 3 and are considered below in greater detail. The phases hitherto recognized, apart from those of termite mounds, are the following:

Drained 1 (Il/Dr 1)	Impeded 2 (Il/Id 2)
Drained 2 (Il/Dr 2)	Impeded 3 (Il/Id 3)
Impeded 1 (Il/Id 1)	Undrained (Il/U)

Termite mounds on the illuvial complex

The frequency with which termite mounds occur on some of the illuvial phases, and their effect on the floristic composition and physiognomy of the vegetation, are often at least as great as the frequency and effect of the E/Dp+ phase on the eluvial complex. On parts of the Il/Id 1 phase the bulk, and on parts of the Il/Id 2 phase nearly the whole, of the woody vegetation appears to depend for its existence on the activity of termites in providing sites above flood level. That this factor of elevation of the ground is the decisive one is suggested by the occurrence of similar patches of woody growth on elevated ground

Table 3. *Composite catena; soils and vegetation of the illuvial complex*

In the third column, species in each group (canopy trees, shrubs, etc.) are listed in approximate order of importance. The record of characteristic undershrubs, grasses and herbs is liable to be incomplete.

Soil phase	Vegetation	Characteristic species
Illuvial drained 1 (upper) Il/Dr 1 Comparatively well drained, upper phase of illuvial complex, on similar topographical level to Il/Id 1, but ground is flat, not uneven. Brownish grey or grey, rather dark-coloured soil, with considerable fine sand fraction	Trees deciduous, medium-tall, spaced so as to resemble an orchard, up to 11 m. (35 ft.) high. Tall grass, 1·5–2 m. (5–6 ft.) high, dense, on flat ground between trees, sometimes with other small trees and shrubs	Dominant 'canopy' trees: *Terminalia macroptera* *Terminalia laxiflora* and/or *Pseudocedrela kotschyi* Small trees and shrubs (frequently absent): *Sarcocephalus esculentus* *Gardenia erubescens* Grasses: *Hyparrhenia rufa* Other *Hyparrhenia* spp.
Il/Dr 1+ (Soil not examined. Termite mounds rarely observed on the Il/Dr 1 phase)	Groups of deciduous and evergreen trees and shrubs, similar to those (Il/Id 2+) on the Il/Id 2 site	As for Il/Id 2+ (below) but usually without *Mitragyna inermis*
Illuvial drained 2 (lower) Il/Dr 2 Similar to Il/Dr 1 but on a slightly lower topographical level, and somewhat less drained	Trees absent except on termite mounds (Il/Dr 2+) which may or may not be present. General type is pure perennial grassland, grass 1·5–2 m. (5–6 ft.) high in tufts spaced 15–20 cm. (6–9 in.) apart, with a variable mixture of tall herbs	Trees and shrubs: None Grasses: *Hyparrhenia rufa* Other *Hyparrhenia* spp.
Il/Dr 2+ (Soil not examined.) Termite mounds built up on the Il/Dr 2 phase	Groups of deciduous and evergreen trees and shrubs, similar to those listed below for Il/Id 2+, on termite mounds which often occur along the margins of the open grassland, but which rarely extend far into it (except when accompanied by intrusions of the Il/Id 2 type of site)	As for Il/Id 2+, but usually without *Mitragyna inermis*
Illuvial impeded 1 (upper) Il/Id 1 Topographically highest of the impeded illuvial phases. Uneven surface and impeded drainage. Greyish buff, light-coloured soil	Canopy trees, deciduous, 9–15 m. (30–50 ft.) high, on elevations in the ground. Sub-dominant trees deciduous, chiefly on fringes of tree-groups. Shrubs, deciduous and evergreen, under shade. Tall perennial grass, 1·5–2 m. (5–6 ft.) high, dense in shallow depressions between groups of trees, less dense beneath shade. Occasional shrubs and small trees on better-drained parts of depressions	(i) On elevations in the ground, not necessarily derived from termite mounds: Canopy trees: *Anogeissus schimperi* (dominant) *Combretum binderanum* *Pterocarpus abyssinicus* *Balanites aegyptiaca* Sub-canopy trees and large shrubs: *Diospyros mespiliformis* *Dalbergia melanoxylon* *Tamarindus indica* *Randia nilotica* Shrubs and scramblers: *Boscia senegalensis* *Capparis rothii* (ii) On better-drained parts of depressions: no species characteristic; see Table 13 (p. 74) for occurrence (iii) In depressions: Tree: *Acacia seyal* (local) Grass: *Andropogon gayanus*

Table 3 (*continued*)

Soil phase	Vegetation	Characteristic species
Il/Id 1 + (Soil not examined.) Termite mounds built up on the Il/Id 1 phase	Groups of trees, usually more luxuriant and with denser undergrowth than on the elevations without termite mounds. This type occurs only in the upper, better-drained part of the phase, represented by Transect III, section VI (p. 70)	As on the elevations in the ground listed under Il/Id 1, with the addition of: Trees: 　*Lannea schweinfurthii* 　*Sterculia setigera* 　*Acacia campylacantha* Shrubs: 　*Maerua harmsiana* 　*Grewia villosa*
Illuvial impeded 2 (lower) Il/Id 2 Similar to Il/Id 1 but on a slightly lower topographical level, with drainage-impedance nearer the surface, which is less obviously uneven. Brownish grey or grey, rather dark-coloured soil	Trees deciduous, medium-tall. Single trees or groups of trees up to about 12 m. (40 ft.) high, on elevations in the ground, too discontinuous to form a canopy. Frequent termite mounds (Il/Id 2 +) bearing deciduous and evergreen trees and shrubs (see below). Tall grass, 1·5–2 m. (5–6 ft.) high, dense, on flat or uneven ground between the elevations, with occasional shrubs in better-drained parts	Large trees: 　*Mitragyna inermis* 　*Acacia sieberiana* Small trees and shrubs: 　*Bauhinia thonningii* (in open) 　*Acacia seyal* (in local depressions, really Il/Id 3) Grass: 　*Vetiveria nigritana*
Il/Id 2 + Termite mounds frequent on the Il/Id 2 phase, built up on the larger elevations in the ground	Dense groups of deciduous and evergreen trees and shrubs, some characteristic, many also characteristic of termite mounds in other zones	Canopy trees: 　*Anogeissus schimperi* 　*Acacia campylacantha* 　*Acacia sieberiana* 　*Diospyros mespiliformis* 　*Lannea schweinfurthii* Sub-canopy trees, shrubs and scramblers: 　*Andira inermis* 　*Cassia singueana* 　*Ziziphus abyssinica* 　*Ziziphus mauritiana* 　*Antidesma venosum* 　*Cissus quadrangularis* 　*Combretum aculeatum*
Illuvial impeded 3 Il/Id 3 Dark grey, fine-textured soil with strongly impeded drainage, on 'partial basin sites'. Reaction slightly acid (cf. Il/U)	Thorny trees 3–9 m. (10–30 ft.) high, usually gregarious, on the site or round its edges. Tall grass of varying density	Tree: 　*Acacia seyal*
Illuvial undrained Il/U 'Black cotton-soil' of basin sites with no drainage. Very dark grey; clod structure; alkaline	Thorny trees, not always present. Perennial grass, often as spaced tufts with much bare ground. In extreme cases soil completely bare	Tree: 　*Acacia seyal* (sometimes absent)

(True basin sites occur only at and outside the northern fringe of the region discussed.)

which to all appearances cannot be of termite origin (p. 75, para. (vii)). Several species of trees and shrubs regularly occur at definite levels in the micro-relief due to mounds, and this regularity is a notable feature of the vegetation of the flood-plain region in particular. The very marked rarity of termite mounds on the drained as compared with the impeded illuvial soils suggests some connexion with their primary difference in nature of surface (even or uneven) and of drainage; the connexion, however, may well be indirect, acting perhaps through some resultant difference in soil properties or possibly fire-incidence.

Comment has already been made (p. 13) on the comparison between mounds of the eluvial and illuvial complexes in the matter of conditions operating and floristic composition resulting.

Description of illuvial phases

Illuvial drained 1 *(Il/Dr* 1)

This upper phase of the illuvial drained group is widespread where the low-level ground is free from undulations. The surface horizon of the soil is greyish brown or grey when dry, and there is some redistribution of iron at a depth of about 30 cm. (12 in.), showing drainage-impedance farther from the surface than in the illuvial impeded phase Il/Id 1 which occupies a corresponding topographical level. Two factors are dominant in the formation of Il/Dr 1 soil, and control its distinctive vegetation; an annual flood of rather long duration which is probably not a static flood but moving, however slowly; and secondly, fairly good aeration after the flood has receded. The conditions of flooding, including probably frequent variation in depth of the flood water, presumably account for the non-accumulation of the finest material and consequently for the large proportion of sand found in these soils.

With alternation between floods and effective drainage, the vegetation is subject to an exceptionally wide variation in water conditions. Furthermore, its site on the edge of the grazing-grounds of pure grassland, which are fired every year, subjects the plants to very powerful fire-selection. These special conditions reduce the characteristic trees to three species in only two genera. The most frequent and regularly occurring species is *Terminalia macroptera*, with or without *T. laxiflora* and *Pseudocedrela kotschyi*. One or both of the two latter (sometimes with *Gardenia erubescens*, a low, shrubby tree, beneath) often form a more or less defined zone in the upper and apparently better drained examples of the type. The appearance of this very open woodland often recalls that of an orchard. Thick-boled, rough-barked, blackened trees stand apart as though evenly spaced, in a dense growth of tall grass (largely *Hyparrhenia rufa*) resembling a grain-crop in its size and spacing (Phot. 11).

Termite mounds (Il/Dr 1+), erected on the flat ground, occur rarely. These carry the usual clump of evergreen and deciduous trees, chiefly species which are also characteristic of the Il/Id 2+ phase (Table 3) and which bear no close relation to the community on the surrounding flat ground.

Illuvial drained 2 *(Il/Dr* 2)

This is the phase occurring next below Il/Dr 1, usually between the latter and a main or subsidiary drainage channel. It also sometimes occurs between Il/Id 2 and a drainage channel. Il/Dr 2, although subject to more prolonged flooding than Il/Dr 1, is likewise drained without marked stagnation, and the surface dries thoroughly in the dry season. As in Il/Dr 1, the ground is free from undulations. The soil is brownish grey or grey when dry, with iron-mottling at less than 30 cm. (12 in.) from the surface.

The vegetation is tall grass, the open plain often continuing for several kilometres bare of trees and shrubs, whose absence is probably due to the combination of flooding and fire. The lower horizons of the soil never dry out completely, and after fire a fresh, green growth of grass soon appears from the old tufts, providing the reason for the firing of the old dry grass by the Dinka herdsmen in need of new grazing for their cattle. As far as could be ascertained from their state in the dry season, the grasses most regularly occurring in the association are *Hyparrhenia rufa* and *Andropogon gayanus*.

An Il/Dr 2+ phase of termite mounds, similar to Il/Id 2+, and bearing a similar mixture

of species, sometimes occurs on the Il/Dr2 phase, chiefly near its upper edge which is free from the deepest and longest-lasting floods, but termite mounds here usually represent an extension of the Il/Id2+ phase from an adjacent zone of Il/Id2 (Phot. 35).

Illuvial impeded 1 (Il/Id 1)

This, topographically the highest phase of the impeded illuvial group, occurs as an alternative to Il/Dr1, just below the Col-Il transition zone already described. The Il/Id1 soil is partly river-flooded and partly rain-flooded, and is affected by considerable and repeated rise and fall in flood-level, which doubtless accounts for its distinctly washed appearance. It is largely composed of colluvial material from the slopes just above, but has some admixture of alluvial deposits. The upper horizon is distinctly colluvial in appearance, with much fine red material partly masked by grey alluvial mixture, while in the lower horizons there is a fairly thick zone showing sparse pea-iron concretions and indications of impeded drainage. The surface of the site is characteristically uneven, with elevations and depressions every few metres. The elevations nearly all show signs of termite activity and often bear termite mounds (Il/Id1+), while the depressions develop a soil approaching that of a partial basin site (see Il/Id3, p. 31). In many of the depressions are holes (locally called 'wongs') resembling swallow-holes, 30–60 cm. (1–2 ft.) across and about 60 cm. (2 ft.) deep, containing lumps of clay which often have a concave top and are partly separated, as though shrunk away, from the walls of the cavity (Phot. 33). These holes also occur in the depressions on the Il/Id2 site, and appear to be associated with local rather than general drainage.† Owing to its undulations, it is scarcely possible to represent the Il/Id1 phase by a single type of site, but for soil-sampling purposes the intermediate level between the elevations and depressions was taken to represent this phase in general terms.

At first glance the vegetation (Phot. 29) is a slightly open, uniform woodland of *Anogeissus*, but in detail it is strikingly different on the elevations and in the depressions. The former bear groups of trees, *Anogeissus* being characteristic and dominant, with other deciduous trees occasional in the canopy, and with several species of evergreen trees and shrubs as understory, mainly on the fringes of the tree-groups. The depressions bear tall grass about 1·5 m. (5 ft.) high, either alone or sometimes, toward their edges, with a few small trees of *Acacia seyal*, a species characteristic of partial basin sites (Il/Id3, p. 31) and often occurring around the base of the larger termite mounds. The Il/Id1 woodland, in its localization of tree growth to elevated sites, presents a parallel case to the E/Dp+ termite-mound communities in the E mosaic, although the existence of a higher plant community on the elevations of the Il/Id1 site is evidently favoured by better drainage in the wet season, instead of by moister soil in the dry season as is doubtless the case with E/Dp+.

On almost imperceptible slopes, as at Aweil (Transect III), this Il/Id1 *Anogeissus* woodland may be very extensive; on short, steeper slopes, as at Wau (Transect I), it was not observed, and the conditions for its existence may be absent altogether. At Halima (Transect II) it was mixed in a narow belt with species characteristic of Il/Id2 and Il/Dr1.

It is difficult to differentiate between the vegetation of the definite termite mounds

† Mr H. C. Dawkins informs us that on better-drained sites in Uganda, holes such as these are left after the collapse of termite mounds. We saw no direct evidence of such an origin.

(Il/Id 1+) and the Il/Id 1 vegetation proper; in the upper part of the Il/Id 1 phase (Transect III, section VI) all degrees of elevation occur, from small or extensive areas raised by only a few inches above the peripheral level of the depressions, to definite mounds up to 1·2 m. (4 ft.) or more in height. In the lower part of Il/Id 1, however (Transect III, section VII), no definite termite mounds were observed, and the species which occurred on the numerous low elevations here are therefore considered to be representative of the Il/Id 1 type (Table 3, p. 27).

Iluvial impeded 2 (Il/Id 2)

This phase, normally next below Il/Id 1, occurs on sites with similarly uneven, though usually less pronounced, micro-relief, or on slightly concave sites with drainage limited accordingly. The soil is darker in colour and considerably finer in texture than in Il/Id 1, while the iron redistribution horizon is thicker and comes nearer to the surface than in the drained illuvials Il/Dr 1 and Il/Dr 2.

Owing to the marked effect of slight differences of level on the degree of flooding, an elaborate mosaic of vegetational units is found. The low elevations, or the sides of these when, as often happens, they are surmounted by large termite mounds (Il/Id 2 +), are occupied by trees of *Mitragyna inermis*. In the better-drained level parts *Bauhinia thonningii* occurs as isolated shrubs. The shallow depressions generally bear only tall perennial grass, but where they form local basin sites (Il/Id 3-Il/U), *Acacia seyal* is often gregarious. Where the Il/Id 2 site covers a considerable area, the upper, better-drained part shows a dominance of the Il/Id 2+ termite-mound vegetation of *Anogeissus, Acacia campylacantha* etc. (Table 3, p. 27), with *Bauhinia* dotted in the higher parts of the grass hollows between (Phot. 31); the lower part shows a gradual diminution in the number of termite mounds, which are progressively taller (standing in the flood in the wet season), while *Acacia* spp. and *Mitragyna* become more frequent (Phot. 34), until the edge of the open grassland of the Il/Dr 2 phase is reached (Phot. 35). The ground here, if uneven, is dotted with lone *Mitragyna* trees, which seem to be favoured by the conditions on the edges of depressions and water-holes. A pure stand of *Mitragyna*, in a much narrower and denser belt, is often seen on the raised ground forming 'levées' behind the banks of rivers, where the drainage conditions are comparable. The grass which appears to be typical of the *Mitragyna* level on uneven ground, and of the open grassland on similar sites, is *Vetiveria nigritana*, in contrast to *Hyparrhenia rufa* on the flat (Il/Dr 2) sites.

Extensive impeded illuvial sites were seen bearing *Mitragyna* or *Bauhinia* as the sole woody species.

Illuvial impeded 3, or partial basin site (Il/Id 3)

Concave sites in which drainage, though markedly impeded, is not completely lacking as it is in basin sites (Il/U, below), are conveniently described as partial basin sites. Concave sites of varying extent can occur anywhere in the illuvial mosaic and even, though more rarely, as intrusions of illuvial character in the midst of eluvial or colluvial areas. In proportion as these concave sites are large or small, they approximate more or less to a true 'black cotton-soil' character in both appearance and soil reaction. True basin sites of any size are rare in the country south of the river Lol, the rainfall being sufficient to give rise as a rule to more or less developed drainage systems, and the

Il/Id 3 phase rather than Il/U is therefore usual. The soil of partial basin sites, although it resembles that of true basin sites in being dark in colour and in losing a large part of its flood water by evaporation, is definitely acid in reaction. The sites display in them or round their edges the characteristic *Acacia seyal* with tall, perennial grass (Phot. 32). An example was seen (on the Chel toich west of Nyamlell) of an extensive stand of *A. drepanolobium*, whose soil requirements are undoubtedly rather similar to those of *A. seyal*, next to a large area dominated by the latter.

Illuvial undrained, or basin site (Il/U)

Extensive examples of the true basin site—the extreme phase of the impeded series— frequently occur north of the river Lol, and more especially north of the Bahr el Arab, in country of low rainfall where the run-off is often not sufficient to cut its own drainage route. The soil, frequently called 'black cotton-soil', is uniform dark grey or black in colour; it has pronounced clod-structure, is alkaline, and often includes calcium carbonate concretions. The vegetation may be pure, or almost pure, gregarious *A. seyal* over tall perennial grass, or grass may be present alone, or in extreme cases the soil may be completely bare.

Riparian sites

None of the transects recorded in detail included a perennial river or stream. Observations of a preliminary nature on river-bank vegetation were made in various parts of the country, but the subject is clearly somewhat independent and is not dealt with in this paper.

CATENA-VARIANTS AND THEIR FLORISTIC RELATIONSHIPS

That the catena, as described in the foregoing pages and illustrated in Fig. 2, is a composite one derived from manifestations in different places, has already been made clear (p. 14), and attention has been drawn in passing to details which vary with conditions of topography and rainfall. The three main observed variants of the catena—connected, naturally, by intermediates—are named after the corresponding transect-localities, Wau, Halima and Aweil. Their distribution in so far as known, and their relation to the two natural regions concerned and to the rainfall belts, are indicated on the map (p. 9). From this it can be seen that the Halima variant preponderates in the higher and the Wau variant in the lower part of the main tributary-river region, while the Aweil variant follows one edge of the flood-plain region. The relation between these regions and the variants is of course extremely close, but the recognition of the variants themselves, as distinct from the respective regional belts of country where they normally occur, is important in understanding the soil-vegetation system met with in any particular place.

Different forms of soil catena, determined by rainfall and nature of immediate parent material, have been recognized in the southern Sudan by Greene (1939, 1945). His four specified catenas cover a wider range of country and conditions than our three variants do; the latter, in fact, are all subdivisions of one of his catenas—the 'toich catena'—and include vegetation as well as soils.

Wau catena-variant

Country like that just east of Wau, where topography and rainfall conditions are intermediate between the extremes of the regions studied, gives the clearest single display of all three complexes; as the two following paragraphs show, conditions towards either extreme of topography and rainfall elaborate one part of the catena and suppress another. The Wau variant also shows the clearest development of the eluvial complex; the higher ground is broad enough for its micro-relief to vary repeatedly but not so flat as to make such variation insignificant. Over the same range of country there is a relative abundance of evergreen trees, which are important through their marked influence on subordinate vegetation; they are much rarer on the eluvial complex where the rainfall is either higher or lower than 1100 mm. (43 in.) annually. In the valleys the Wau variant presents an illuvial complex whose drained (Il/Dr) phases are very pronounced, but valley-margins, as opposed to flood-plain margins, seem to be free of prolonged drainage-impedance; rarely, if ever, do they show full development of the impeded illuvial group (Il/Id).

Halima catena-variant

Conditions such as those at Halima (Ngowlima)—narrower and steeper ridges and somewhat higher rainfall—cause more downward movement of eroded material. On the eluvial complex, the result is to leave soils which are coarser-grained than in the other variants, and because of this influence towards soil uniformity, and the comparative narrowness of the ridges, the clarity of the eluvial mosaic is reduced. On the lower slopes, if they are long enough and not too steep, the plentiful eroded material is sorted out over a broad colluvial belt, producing the most marked development of the colluvial sub-catena. Vegetationally the effect here is, as a rule, shown largely by an extension of the familiar association of fire-resistant *Combretum* species on the soils described as Col/F 1, but there may also be a good representation of the other two colluvial zones already described. The rather narrow valleys, often lacking a flat bottom, do not enable widespread flooding, so that the illuvial complex is usually much restricted or even absent.

Aweil catena-variant

The greatest elaboration of the illuvial complex occurs, naturally enough, in the largely illuvial flood-plain region. Here the low relief and very gentle slopes, little above the level of the large rivers, allow wide spreading of the flood and a maximal influence by its duration and mode of drainage, and the illuvial complex is extensive and diversified accordingly. The lower illuvial belts of the Aweil catena-variant cover the major part of at any rate the north-western end of the flood-plain region; the south-eastern end, which was observed in a much more cursory manner, is probably similar fundamentally. The very slight elevation of the higher ground, and receipt of a lower rainfall than that of the other variants, lead to relatively little erosion; consequently the eluvial soils are (according to general observation) comparatively fine-grained. The flatness of the ground is accompanied by a somewhat simplified eluvial mosaic. The slopes leading down to the flooded levels are so insignificant that the colluvial complex may be scarcely distinguishable, or its lower parts may show signs of impeded drainage near the surface and have much in common with the Col-Il transition zone just below it.

These broad differences in the manifestation of the three complexes (E, Col, Il) are not, of course, the only distinction between the main variants (Wau, Halima, Aweil) of the generalized catena. There are floristic differences. Table 4 shows the species characteristic of the three complexes in each of the three catena-variants—at large, and not only on the respective transects. The species within each classified (habit) group are arranged to show, going down the table, their approximate 'drift' in the sequence Halima → Wau → Aweil variant. Many of these differences, particularly on the eluvial, and to some extent on the colluvial complex, are certain to be due directly to difference in rainfall, but which species are so controlled cannot be stated with any certainty.

A useful floristic comparison of the catena-variants is attained only by considering each complex in turn. As a result of its arrangement for this purpose, Table 4 also provides a general list of species characteristic of each of the three complexes in the country with which this paper deals. In most cases each species is listed for only one complex (E, Col or Il)—that in which its occurrence seems most characteristic—although several species have also been found frequently in one of the other complexes, and a very few occur in all three. For trees and shrubs *characteristic* in the manner explained this list attempts to be comprehensive. The list of undershrubs, grasses and herbs is bound to be incomplete, owing to the limitation of records to three months when the country was dry and much burnt. Those unfamiliar with savanna woodland can gain some idea of what this means from the excellent photographs by Buxton (1935), taken in different seasons in country very like the south-west Sudan. The incompleteness of the list may apply unevenly to the three complexes, and again unevenly to the three catena-variants; in the first case because the E complex, yielding the longest herbaceous list, had in general been subject to less widespread recent burning than the Col and Il complexes, and in the second because examples of the respective variants were examined after different periods since burning, and the subsequent growth had therefore progressed to different degrees. Appreciable recovery was noticeable, for instance, in the Col complex at Halima, compared with its state near Wau when examined 3½ weeks earlier.

IV. DETAILED TRANSECT STUDIES

INTRODUCTION

It has already been indicated that the first requirement, in analysing the frequently confused pattern of soils and vegetation, is recognition of type-units of the lowest category in which they are clearly defined, i.e. phasic units. Before this stage was fully attained in our own work in the field, including that done on previous journeys in the Sudan by one of us (C. G. T. M.), satisfactory understanding of the pattern and relationships was not achieved. Much time and effort could have been saved if, at the outset, a clear idea had been available of the nature of the fundamental soil-vegetation units. The only really satisfactory way of appreciating these entities, especially where the relatively clear zonal form is replaced by confusing mosaics, is by introduction to them in the field. The next best course is presentation of field records, with photographs of the actual sites. In the hope that they may assist future field work dealing with similar country, these records are given in the following pages. From this standpoint, attention may be drawn

Table 4. *Species characteristic of the eluvial, colluvial and illuvial complexes in the Halima, Wau and Aweil catena-variants*

+ Occurrence characteristic.

(—) Characteristic occurrence expected on grounds of general observation of the species, but not actually noted, probably through seasonal or burnt state causing difficulty in recognition.

— Occurrence not characteristic; in many cases not observed at all.

* before plant name: Characteristic of termite mounds.

	Halima variant Steepest topography; highest rainfall	Wau variant Intermediate topography and rainfall	Aweil variant Flattest topography; lowest rainfall
Eluvial (E) complex			
Canopy trees, and lianes (TL):			
Isoberlinia doka	+	—	—
Erythrophleum africanum	+	—	—
Cordyla richardii	+	—	—
Afzelia africana	+	+	—
Burkea africana	+	+	—
Prosopis africana	+	+	—
Parinari curatellifolia	+	+	—
Amblygonocarpus schweinfurthii	+	+	—
Daniellia oliveri	+	+	—
Manilkara schweinfurthii	+	+	—
Terminalia mollis	+	+	—
*Landolphia spp. (TL)	+	+	—
Lannea kerstingii	+	+	—
Afrormosia laxiflora	(—)	+	—
*Khaya senegalensis	+	+	+
*Hippocratea richardiana (TL)	+	+	+
Lannea schimperi	+	+	+
*Opilia celtidifolia (TL)	(—)	+	+
Sclerocarya birrea	—	—	+
Albizzia sericocephala	—	—	+
Sub-canopy or small trees and large shrubs:			
*Mystroxylon aethiopicum	+	—	—
*Maba abyssinica	+	+	—
*Teclea nobilis	+	+	—
Hexalobus monopetalus	+	+	—
*Boscia salicifolia	+	+	—
Strychnos spinosa	+	+	—
Oncoba spinosa	+	+	—
Detarium senegalense	+	+	—
Landolphia comorensis var. florida	—	+	—
Maerua angolensis	—	+	—
Gardenia lutea	—	+	—
Strychnos innocua	+	+	+
*Diospyros mespiliformis	+	+	+
Crossopteryx febrifuga	+	+	+
*Ximenia americana	+	+	+
Hymenocardia acida	+	+	+
Lonchocarpus laxiflorus	+	+	+
Combretum verticillatum	+	+	+
C. ghasalense	—	+	+
C. lecananthum	—	+	+
Small shrubs and scramblers:			
*Popowia djurensis	+	+	—
*Rhus natalensis	+	+	—
Gardenia triacantha	+	+	+
*Adenia venenata	—	+	+
*Capparis corymbosa	—	(—)	+
Undershrubs, grasses and herbs:			
Striga barteri	+	(—)	(—
Ctenium elegans	+	+	(—
Barleria grandicalyx	+	+	—
*Wissadula amplissima var. rostrata	(—)	+	—
Indigofera binderi	(—)	+	—
Xysamlobium heudelotianum	(—)	+	—
Indigofera bongensis	(—)	+	—
Courbonia virgata	+	+	+

Table 4 (*continued*)

	Halima variant Steepest topography; highest rainfall	Wau variant Intermediate topography and rainfall	Aweil variant Flattest topography; lowest rainfall
Undershrubs, grasses and herbs (*continued*):			
Urginea spp.	+	+	+
Hyparrhenia barteri var. *calvescens*	(—)	+	(—)
Bulbostylis coleotricha	(—)	+	(—)
Sporobolus sp. (*festivus?*)	(—)	+	(—)
Indigofera bracteolata	—	+	—
Lepidagathis sp. aff. *fischeri*	—	+	—
Ammocharis tinneana	(—)	+	+
*Beckeropsis uniseta	(—)	(—)	+,

Colluvial (Col) complex (including Col-Il transition)

Trees, large shrubs and bamboo:			
Oxytenanthera abyssinica	+	—	—
Hymenocardia acida	+	+	—
Pterocarpus abyssinicus	+	+	—
Acacia seyal var. *multijuga*	+	+	—
Butyrospermum parkii var. *niloticum*	+	+	+
Gymnosporia senegalensis	+	+	+
Combretum undulatum and/or *C. glutinosum*	+	+	+
C. ghasalense† and/or *C. verticillatum†* and/or other *Combretum* spp.†	+	+	+
Entada sudanica	—	+	+
Small shrubs, undershrubs, grasses and herbs:			
Lepidagathis appendiculata	+	—	—
Indigofera hendecaphylla	+	—	—
Euphorbia bongensis	+	—	—
Cochlospermum tinctorium	—	+	—
Hyparrhenia rufa and/or *Andropogon gayanus*	(—)	+	+

Illuvial (Il) complex

Principal or large trees:			
Terminalia laxiflora	+	+	—
T. macroptera	+	+	+
Mitragyna inermis	+	+	+
Anogeissus schimperi	+	—	+
Pseudocedrela kotschyi	+	(—)§	+
Acacia seyal	—	+	+
*Lannea schweinfurthii	—	+	+
Combretum binderanum	—	—	+
Balanites aegyptiaca	—	—	+
Acacia sieberiana	—	—	+
Subsidiary or small trees, large shrubs and scramblers:			
Gardenia erubescens	+	+	—
Sarcocephalus esculentus	—	+	+
Bauhinia thonningii	—	—	+
Dalbergia melanoxylon	—	—	+
Randia nilotica	—	—	+
*Acacia campylacantha	—	—	+
*Ziziphus abyssinica	—	—	+
*Z. mauritiana	—	—	+
*Andira inermis	—	—	+
*Cassia singueana	—	—	+
*Cissus quadrangularis	—	—	+
*Combretum aculeatum	—	—	+
*Capparis rothii	—	—	+
Small shrubs, undershrubs, grasses and herbs:			
Hyparrhenia rufa and/or any or all of: *Andropogon gayanus*, *Vetiveria nigritana*, *Hyparrhenia dissoluta*	(—)	+	+
*Boscia senegalensis	—	—	+
*Maerua harmsiana	—	—	+
*Grewia villosa	—	—	+
*Antidesma venosum	—	—	+

† These *Combretum* species sometimes occur also on the E or Il complex, but are abundantly represented on the Col complex, either alone or as a group of species.

§ Failure to observe *Pseudocedrela*, expected here, probably due to its elimination as timber.

to the recorded approximate lengths of the sections into which the transects were divided, especially where, as was usual, one section represented one soil phase and its vegetation. As a consequence of the choice of transect sites, these section-lengths nearly all represent widths of zoned soil-vegetation units, and it may be noted that the zones can be very narrow. On the whole, more extended zones were the rule, narrow zonation being a factor favouring transect-selection. The data put forward do not purport to show the best method of recording the required information. With gain of experience and ample time in the field, greater objectivity and precision are possible, as well as more numerous samples. Accurate levelling is needed on the flatter sites.

This final part of the paper also discusses soil and vegetation data applying to the particular sites studied, and in so doing amplifies some of the points hitherto presented in more general terms, especially with regard to soil analysis results (pp. 39, 44, 52, 61, 72) and the influence of termite mounds and of fire (p. 56).

The first close study was the examination of Transect I, a little to the north-east of Wau, with a rainfall of about 1100 mm. (43 in.). The comparatively simple and distinct zonation, representing all three complexes, which was seen here (Phot. 4) and confirmed and amplified by observations farther to the north-east along the Wau-Meshra road, proved to be the key to the whole confusion of soil and vegetation types.

The observations made on the eluvial mosaic in Transect I, section I (p. 42), were amplified by records taken on a similar area of ironstone woodland 2 or 3 km. away on the same ridge. These records are given separately (p. 49 and Tables 8 and 9 following).

After the investigation of Transect I, a somewhat rapid but extensive tour was made through the western part of the main tributary-river region, as far as the western jebel region about the head waters of the River Boro, and notes were taken on the differences in soil and vegetation, undoubtedly induced very largely by the higher and more dissected relief and greater rainfall. The variants observed, although often not conforming closely to the Wau catena-variant, were seen to be of the same fundamental nature and, in places where the topography happened to be similar, the Wau zonation was sometimes repeated.

An accessible place with vegetation of the more luxuriant, western type (later also observed towards the south) was found only about 25 km. (15 miles) south-west of Wau, in the rather hilly locality at Halima (Ngowlima), and it was studied in some detail (Transect II). This transect provided good supplementary information on the colluvial sub-catena. The eluvial site was on a ridge presenting micro-relief strikingly different from that of the high-level site in Transect I, and showed signs of receiving a somewhat higher rainfall. The low-level, illuvial types were very poorly represented but nevertheless recognizable in a contracted and confused form.

After studying the first catena-variant close to Wau and the second, with higher relief and rainfall, farther west and at Halima, attention was directed to the effect of lower relief and lower rainfall, which are normally co-existent. A suitable area, exemplified by Transect III, was found close to Aweil, about 140 km. (90 miles) north-west of Wau. The area comes within the flood-plain region, but only part of it is below the normal flood level. The mean annual rainfall at Aweil, according to data so far available, is about 1000 mm. (40 in.), and the dry season is a little longer than at Wau.†

† Published rainfall records for Aweil, which cover only the years 1932–7, give a mean annual value of 1010 mm. The corresponding figure for the same period at Wau is 1069 mm.—a comparatively small

The eluvial mosaic is simplified by the comparative shortage of evergreen canopy trees; the colluvial sub-catena is much confused and in places practically eliminated by the absence of sufficient slope; and the illuvial mosaic is extended and complicated by the characteristically almost flat relief of the margins of the toich (flood-plain grassland), which forms an irregularly broad belt beside the course of the River Lol.

The three transects, with the additional study of the eluvial mosaic near Transect I, together provide specimen data on soils and vegetation covering practically the whole of the composite catena. Some of the examples merge two or more phases together, but most of the phases have separate examples. Only Il/U (basin sites), and termite mounds on the levels where they occur infrequently, are not represented at all. Table 5 shows in summarized form the phases which, with their vegetation, were represented in the separate transects. More precise details are given in the transect descriptions and their associated tables.

Table 5. *Representation in the transects of phasic units of the complete (composite) catena*

+ indicates the collection of data; soil description and vegetation records were made in all these cases, and soil sampling and analysis in most.

} + indicates that the phases listed opposite the bracket occurred as a mixed type, or that their vegetation was recorded as bulked data.

Phases of complete catena	Transect I (Wau)	E mosaic near Transect I	Transect II (Halima)		Transect III (Aweil)
			Upper catena	Lower catena	
E/Dp+	· ⎫	+	·	·	· ⎫
E/Dp	· ⎪	· ⎫	·	·	· ⎪
E/S	· ⎪	· ⎬ +	+† ⎫	·	· ⎬ +
E/S.R	· ⎬ +	+	· ⎬ +	·	· ⎭
E/S.Er	· ⎪	·	+† ⎭	+	·
E/O	· ⎭	·	·	·	·
E-Col	·	·	+	·	·
Col/C	· ⎫	·	·	+	·
Col/F 1	· ⎬ +	·	+	+	+
Col/F 2	·	·	·	+	·
Col-Il	+	·	·	·	+
Il/Dr 1	+	·	·	· ⎫	·
Il/Id 1	·	·	·	· ⎬ +	+§
Il/Id 2	·	·	·	· ⎭	+§
Il/Id 3	·	·	·	·	+
Il/Dr 2	+	·	·	·	+
Il/U	·	·	·	·	·

† These two phases here occurred together as an intermediate type.
§ With Il/Id 1 + and Il/Id 2 + respectively.

RECORDING OF TRANSECTS

The transects were located in what appeared to be representative areas, subject to the vegetation being as little spoilt and the types as clear-cut as possible. Places obviously not typical, or showing signs of recent cultivation, were avoided. Each of the three transects was sited so as to run down the general direction of a slope, starting in the eluvial complex, crossing the colluvial, and ending in the illuvial. This layout did not, of course, apply to the purely eluvial area separately studied, but the other details of

difference from which, however, little can be argued owing to the short period involved. In three consecutive years (1932–4) Aweil received a greater total rainfall than Wau, the total in 1934 being as much as 138 mm. higher at Aweil. In each of these three years, however, as well as in the three following years of the comparable period, the number of days in the year with a rainfall of 1 mm. or over was higher at ·Wau, with a mean number of 79·7 such days as against 62·3 at Aweil.

working were the same for it (*mutatis mutandis*) as for the transects themselves. With few exceptions, soil-pits were dug and sampled, and records of the vegetation were made afresh, in each section which appeared to represent a distinct vegetational unit. With the siting of the transects in the manner described, these units were usually zoned, so that the width of the zone was recorded as the length of the section; its lateral extension was indefinite. In listing the species, the width of the transect was necessarily varied from section to section according to the kind of vegetation and its condition; in some places burning had been so thorough that a fairly wide inspection was needed before a reasonable proportion of the flora could be identified. Under these circumstances retention of a straight line was impossible. The frequency and height of species were estimated by eye; the heights were afterwards checked as far as possible with the aid of photographs.

In describing each section, a brief designation is first given to convey some immediate idea of its most obvious recognition character—normally vegetational; for instance 'Ironstone woodland', '*Combretum* scrub', '*Butyrospermum*', etc. For the soils, the colour in the air-dry state is first given in popular terms, followed in brackets (Ridgway plate – , R. pl. –) by the result of careful comparison of its colour with the plates compiled by Robert Ridgway (1912). These two standards of colour description often fail to tally consistently, probably because a first impression of colour is in fact influenced by texture also. The colour of surface soil samples was in many cases darkened by ash and charcoal from burnt vegetation, rather than by humus.

Soil analysis; general results

The figures given in Tables 6, 8, 10 and 12 refer to analyses of soil from single sites, and must therefore be considered with caution, especially in comparing individual soils (notably their mechanical analysis) from different transects. Rather more reliance can be placed on comparison of phases in the same transect. Descriptions of the horizons sampled appear in the text relating to the transects. In connexion with the analyses the differences in total depth must be borne in mind, the eluvial soils being the shallowest and the illuvials the deepest. Determinations of exchangeable calcium were made for Transect I only. The results, which conform to expectation, receive brief comment on p. 48.

Mechanical analysis

A modified Sudan method was used. The figures represent percentage weight of air-dried fine material. Pea-iron, which is a major component of some eluvial soils, is excluded, and where its amount is very high the figures for mechanical analysis give no indication of the composition of the whole soil. In such cases the sample is indicated by ($\ddagger$) in the tables.

In the great majority of profiles the lower horizons contain decidedly larger amounts of fine material than the surface. This phenomenon is naturally least apparent in the shallowest, that is, the eluvial, soils. It also seems less evident on Transect I, near Wau, than on the much flatter topography of Transect III at Aweil.

In general, as would be expected, the soil texture becomes finer from the eluvial down to the illuvial complex, although irregularity in the progression is introduced by the drained illuvials, whose clay-accumulation is limited (Transect I, section IV; Transect II, section X).

The eluvial samples from Aweil are much richer in clay than those from corresponding sites near Wau, E/Dp values derived for comparable depths in these two localities being about 22 and 14% respectively, and E/S.R values 24 and 6%. Some such difference is to be expected, for with very little slope and lower rainfall, eluviation near Aweil is likely to be less pronounced than near Wau. The eluvial soils at Halima, with the greatest

steepness and rainfall, appear to be the poorest in clay, but no quantitative comparison with the above figures can be made, since the same two phases are not distinctly represented in the Halima transect.

A special feature of the Aweil soils is their high content of coarse sand, which may reasonably be connected with the presence of material originally transported from a distance (p. 72).

pH *determinations*

These were made by means of the glass electrode (soil/water ratio 1/2·5) on material which had been dry for many weeks. The results may differ to some extent from the values that would have been obtained had field determinations been possible.

All the soils except those from termite mounds are acid in varying degrees. In the eluvial soils, acidity increases with depth. This seems to be characteristic of tropical soils of this kind, and is confirmed by some unpublished results of H. Greene on soils of a neighbouring region; it is also in keeping with the findings of Doyne (1935). The eluvial soils from Aweil appear rather more acid than those of the other transects. This distinction might seem difficult to explain in view of the somewhat lower rainfall, but it may, like the sand fraction already mentioned, derive from the original transport of material to the neighbourhood.

In contrast to the eluvial soils, the illuvials show decreasing acidity with depth, while the colluvial soils vary in this respect between one site and another and, in at any rate one or two instances, between the upper and lower parts of the same profile.

Clay analysis

The figures are percentages of oxides in the ignited clay fraction. Although incomplete, they show general agreement with those given by Greene (1939). The ratio SiO_2/Al_2O_3 is higher than that associated with lateritic soils according to the suggestions of Martin & Doyne (1927), and on such a basis these soils are definitely not lateritic. It may be noted, however, that if the iron be included the ratio SiO_2/R_2O_3, which may well be a better index figure, is usually below 2. It may be significant that for comparable eluvial soils of the three transects this ratio—1·56 in Transect II, 1·88 in Transect I and 2·14 in Transect III—increases as the rainfall decreases. In general the illuvial soils show the highest values for SiO_2/R_2O_3; the lowest in each transect are shown by the colluvial soils, except for those of the lower catena of Transect II, whence no comparable eluvial values are available. Hence it seems probable that colluvial soils are more thoroughly weathered than eluvials, while illuvials are subject to resilication.

According to the indications so far available, the ratio SiO_2/Fe_2O_3 in the clay fraction is likely to prove useful as a diagnostic figure for the catena sequence (pp. 48, 74).

EXPLANATION OF VEGETATION TABLES

The transects being single samples, it scarcely needs saying that the tables recording their vegetation (Tables 7, 9, 11, 13) do not include all the species collected or observed in the respective localities. A further feature only to be expected is the large number of species in the tables which are not restricted to any particular section (usually a single phase or zone) in a transect. For this, three causes may be distinguished: 'Casual' occurrence at variance with that usual for the species; partiality of certain species to

termite mounds, regardless of their location; and a fairly wide tolerance of conditions by certain species. Amongst the latter, some, like *Bridelia scleroneuroides* and *Grewia mollis*, seem to be characteristic of well-drained sites in general, and especially of secondary growth after cultivation or severe burning, and their distribution is therefore rather sporadic. Of the species of more or less extended occurrence in the catena, a high proportion do, however, show a greater *abundance* in one or a few of the zones, especially if occurrences on the variously sited termite mounds are disregarded. Account has been taken of this fact in arranging the tables by the method explained below. An order of listing results in which the species approximate to what might be termed their average relative position, in their often irregular sequence of occurrence, or 'drift', down the transect.

Arrangement of tables

The sections of the transects are numbered from above downwards, i.e. from eluvial to illuvial.

The order of arrangement of species is governed as follows (with appropriate modifications for Table 9, which records a mosaic site with termite mounds as segregated components). First are given species found only in section I of the transect, then those only in sections I and II, then those only in section II, and so on, with modifications of the same general principle where a species occurs in three or more sections, or in sections which are not contiguous. Where this arrangement produces a block of species common to the same section(s), those of greater importance on account of size or abundance are placed first.

Habit of species

Habit is indicated beside the plant names in the tables by the symbols explained in the following key. Here the term 'tree' is used in the sense of a woody plant 4·5 m. (15 ft.) high or more, whether of tree or shrub habit. The shrub layer is normally considered as any woody growth 1·5–4·5 m. (5–15 ft.) high, and the herb layer as 0–1·5 m. (0–5 ft.), although the limits cannot be used rigidly. Grasses (besides bamboo), for instance, sometimes attain 3 m. (10 ft.), and often 1·8–2 m. (6–7 ft.), thereby exceeding the smaller shrubs.

CT tree forming part of the main upper canopy; occurring as tree only.
CTS canopy tree occurring as such, and also in the shrub or herb layer as saplings or coppice.
T sub-canopy or small tree, or tree forming part of a widely-spaced stand over shrubs or grass; occurring as tree only. Bamboo (*Oxytenanthera*) is included in this category because of its size.
TS sub-canopy or small tree, occurring as such and also in shrub or herb layer as saplings or coppice.
TL liane growing to tree height.
TLS liane growing to tree height, with shrub- or herb-size specimens also present.
Cl climbing shrub or scrambler growing to tree height.
ClS climbing shrub or scrambler growing to tree height, with shrub- or herb-size specimens also present.
S (T) tree occurring as saplings or coppice of shrub or herb size only.
S (TL) liane occurring as shrub- or herb-size specimens only.
S (Cl) climbing shrub or scrambler occurring as shrub- or herb-size specimens only.
S shrub, of shrub or herb size, but excluding true undershrubs.
Us undershrub (suffrutex), of heath-like habit or behaving like a herbaceous perennial, and always of herb size.
G grasses (excluding bamboo (*Oxytenanthera*)).
H herbs (excluding grasses).

Frequency of species

The frequencies indicated, which are subjective estimates, refer only to the portion of the area actually traversed. A species marked 'rare', for instance, may be common in the locality or even close by, but was not so on the transect. Symbols used are:

d dominant cd co-dominant sd sub-dominant a abundant
f frequent o occasional r rare l local(ly)
and combinations of these.

The actual number of individuals is given where the quantity was even less than 'rare', or where the area recorded as a unit (section) was small enough for observation of every individual of relatively conspicuous species. (1 (one) and 1 (local), though similar in print, can when necessary be distinguished.)

ld (locally dominant) is employed in two superficially but not fundamentally different senses. Its usual meaning of local dominance as a society applies to the following trees which are normally gregarious: *Isoberlinia, Butyrospermum, Anogeissus, Terminalia macroptera, T. laxiflora, Mitragyna, Acacia seyal, Hymenocardia* and several *Combretum* species. In other cases, however, it refers to a single tree spreading so as to influence local vegetation, e.g. that of a termite mound or other small community. This use of the term is made necessary because of the great influence of single large trees in the rather dry type of vegetation concerned.

No attempt is made to record the occurrence of grasses or other herbaceous species which were unidentifiable through burning or other causes.

The records of height are given in feet rather than metres, for the convenience of Forest Officers and others in British territories.

TRANSECT I (WAU CATENA-VARIANT)

Date: 12 January 1939.

Location: 5–6 km. (3–4 miles) north-east of Wau; on north-west side of the Wau-Meshra road and about 0·8 km. (½ mile) from it. Line of transect from the sloping edge of a low ridge to the level bottom of a valley with no visible outlet.

Slope: About 1 in 30 in sections I–III; sections IV and V almost level.

Aspect of slope: Approximately south-east.

Length: About 225 m. (250 yd.).

Width: Average 45 m. (50 yd.).

Vertical rise: Not accurately determined; about 6 m. (20 ft.), nearly all occurring in sections I–III.

DESCRIPTION OF SECTIONS

Section 1

Ironstone woodland on mosaic of the E phases (Phot. 8; taken on an adjacent area of closely similar character).

Length 90–140 m. (100–150 yd.). Ground fairly smooth; occasional blocks of ironstone, more frequent towards the lower edge; scattered large termite mounds, of which only one was in the area studied.

Soil. The E/Dp phase only was sampled. 5 cm. (2 in.) litter of dried leaves on the surface.

0–5 cm. (0–2 in.). Dark reddish brown (Ridgway plate† XXIX Bister), sandy loam with some small and medium-sized pea-iron.

5–20 cm. (2–8 in.). Brownish red (R. pl.† XXIX Verona brown), with much pea-iron grading into larger agglomerations below.

20–35 cm. (8–14 in.). Similar to above but with larger agglomerations up to 10 cm. (4 in.) in diameter.

35 cm. (14 in.) —. Very hard, compact ironstone with vesicular structure. Very red in the upper layers but becoming yellower and softer with depth.

Vegetation. Deciduous woodland, almost leafless at this season with the exception of a sprinkling of evergreen trees averaging less than 15% of individuals. General canopy 9–15 m. (30–50 ft.) high, with occasional outstanding trees (usually the evergreens *Khaya* and *Daniellia*) attaining 18 m. (60 ft.). Canopy dense in places but generally rather open, with a considerable admixture of smaller trees and shrubs, some evergreen. Tall grass and herbs occurred thinly throughout, though mostly burnt. The characteristic vegetation-unit of each of the E soil phases was represented, but on this site they were listed jointly. Some of them were studied individually on a nearby site (p. 49).

† Ridgway (1912).

Phot. 9. Transect I (Wau), Section II (Col F1 phase) in foreground; *Pterocarpus* (A), *Butyrospermum* (B), *Combretum* spp. (C).
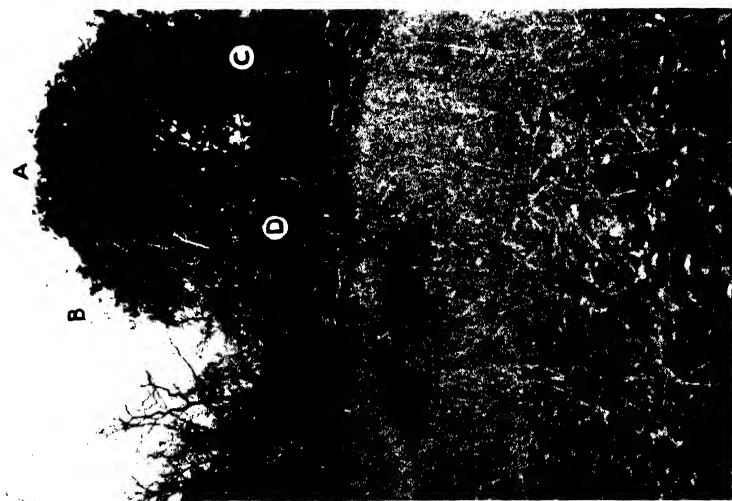
Phot. 8. Adjacent to Transect I (Wau), section I. Large *Daniellia* (A) and *Strychnos innocua* (B) on E.Dp phase; *Butyrospermum* (C) on E.S; *Hymenocardia* (D) and other shrubs, with annual and perennial grasses and herbs, on E.S.Er and E.S.R.

Phot. 10. Transect I (Wau). Left, part of section III (Col-Il transition); centre, section IV (Il/Dr1 phase), with group of *Terminalia laxiflora*; right, burnt open grassland (*Hyparrhenia rufa*) of section V (Il/Dr2-Il/ld3 phase).

Phot. 11. Typical *Terminalia* open woodland, mostly of *T. macroptera*, with grass cover of *Hyparrhenia* spp., on Il/Dr1 phase; beside the Wau-Aweil road.

Section II

Combretum scrub (Phot. 9).

Length 18–65 m. (20–70 yd.), varying along the zone. Ground smooth except for burnt grass-tufts and one old termite mound.

Soil. Col/F 1 phase.

0–12·5 cm. (0–5 in.). Pinkish brown (R. pl. XV Russet), light loam, loose and very porous, with some pea-iron.

12·5–35 cm. (5–14 in.). Reddish brown (R. pl. XXVIII Vinaceous tawny), loose and porous, with increasing amount of similar pea-iron.

35–57 cm. (14–23 in.). Paler, pinkish brown (R. pl. XXIX Orange cinnamon), harder and more compact, with some yellow specks and pea-iron.

57 cm. (23 in.) —. Ironstone, not very hard, mostly yellow. Soil still dry.

Vegetation (Col/C and Col/F 1 type). Widely spaced small trees and shrubs, chiefly *Combretum* spp., some coming into leaf and flower, all sizes from 0·3 to 6 m. (1–20 ft.), many of the smaller ones coppice from cut or burnt stumps. A few outstanding trees of other genera 6–14 m. (20–45 ft.) high, very widely spaced. Ground largely burnt bare, with much ash on the surface, leaving tall grass and remains of herbs only in places. Subdivisions later distinguished as belonging to Col/C and Col/F 1 soil phases were not separately recognized at the time. The list in the table thus includes species not specially characteristic of the Col/F 1 phase from which the soil data were obtained.

Section III

Transition zone (Col-Il) between sections II and IV (Phot. 10, left).

Length 14–18 m. (15–20 yd.). Slope locally slightly steeper in this section, which appeared to lie at the upper edge of the area regularly flooded. Ground smooth except for grass-tufts.

Soil. Not examined.

Vegetation. An open association of mostly isolated shrubs, with patches of exceptionally tall grass, up to 3 m. (10 ft.), left by the recent burning, which was less severe here than in section II. Disregarding *Mitragyna* near a water-hole, there are only six woody species; of these, two (*Grewia* and *Bridelia*) are present in section II, just above, and two (*Terminalia laxiflora* and *Sarcocephalus*) are virtually the only woody members of section IV, just below; from this composition the vegetation acquires its transitional character.

Section IV

Terminalia 'woodland' (Phot. 10, centre).

Length about 18 m. (20 yd.). Slope just perceptible. Slightly higher level than section V. Ground smooth except for grass-tufts and one old termite mound.

Soil. Il/Dr 1 phase.

0–12·5 cm. (0–5 in.). Brown (R. pl. XXIX Sepia) loam, loose and porous.

12·5–30 cm. (5–12 in.). Pale brown (R. pl. XL Avellaneous) loam, compact, with slight iron staining.

30–60 cm. (12–24 in.). Pale greyish brown (R. pl. XXIX Pinkish buff) loam, more compact, with considerable iron mottling.

60–90 cm. (24–36 in.). Grey, compact, with much mottling.

90 cm. (36 in.) —. Grey, compact, and heavier in texture.

Signs of seasonal waterlogging were evident below 30 cm. (12 in.), and the soil was moist below this depth.

Vegetation. Scattered trees of *Terminalia* 8–11 m. (25–35 ft.) high. A very rudimentary example of Il/Dr 1 Terminalietum; 8 trees in all, in three groups of 4, 3 and 1. Tall grass less dense than in section V.

Section V

Valley grassland (Phot. 10, right).

Level bottom of a valley about 140 m. (150 yd.) wide; elongated, but with no definite outlet and therefore tending to be of the nature of a basin site, though better drained in some parts than others. Section V

itself was on a better-drained part. Towards the other side of the valley-bottom the occurrence of occasional trees of *Acacia seyal* suggested inefficient drainage.

Soil. Il/Dr 2-Il/Id 3 phase (intermediate in drainage conditions).

0–12·5 cm. (0–5 in.). Dark grey (R. pl. LI Mouse grey) clay, loose and friable.

12·5–40 cm. (5–16 in.). Grey (R. pl. LI Mouse grey), compact clay.

40–60 cm. (16–24 in.). Grey (R. pl. XLVI Light drab) clay with mottled patches.

60 cm. (24 in.) —. Grey, waterlogged clay.

Vegetation. Tall perennial grass, dense, up to 2 m. (6½ ft.) where not burnt; one species of herb frequent, of similar height, unidentifiable at this season.

SOIL ANALYSIS, TRANSECT I

Section III (Col-Il transition) was not sampled. The data for the other sections are given in Table 6.

Mechanical analysis

With the single exception of the E/Dp soil of section I, the second horizon contains more clay than the surface horizon. This is what would normally be expected; the exception in the case of E/Dp may be due to termite activity, which was very pronounced close to this site.

The Col/F 1 soil of section II shows less variation than any of the others, as between the upper and lower horizons. This would be expected from its position towards the bottom of the slope and the method of its formation.

In section IV (Il/Dr 1) the horizons, though fairly similar, show some slight increase in clay content lower down. The clay content throughout is less than in the Col/F 1 soil of section II. It is not to be supposed that fine particles fail to reach the section IV site, which is topographically lower; what probably happens is that the oscillating valley-flood, meeting the run-off from the colluvial slope on the level of section IV, disperses large amounts of the finer material.

In section V, the soil (Il/Dr 2-Il/Id 3) is very heavy in texture, especially in the lower horizons. This considerable deposition of fine particles could only result from very slow movement of flood water in the valley bottom.

pH *values*

The pH of 6·9 in the surface E/Dp sample from section I is unexpectedly high, possibly owing to local termite activity, but the soil shows the increase of acidity with depth which is very characteristic of certain tropical soils. The samples from section II (Col/F 1) do not show the same regular increase in acidity with depth. This suggests a certain degree of immaturity and would be expected from the colluvial origin.

In section IV the soil (Il/Dr 1) is more acid, the material being exposed to considerable leaching, first of all in its passage to the site, and subsequently by the oscillating flood which has already been suggested as responsible for the texture. The increase in acidity with depth shows that this site is comparatively freely drained, although it is saturated in the wet season. In section V (Il/Dr 2-Il/Id 3), on the other hand, while the surface soil is if anything more acid than that of section IV, the lower horizons show a reduced acidity. This indicates greater drainage impedance, which was indeed a feature of the site.

Table 6. *Transect I (Wau); soil analysis*

Soil phase	Section I E/Dp			Section II Col/F1			Section IV Il/Dr1			Section V Il/Dr2-Il/Id3		
Vegetation type	Ironstone woodland			Combretum			Terminalia			Valley grassland		
Cm. from surface	0–5	5–20	20–35	0–12.5	12.5–35	35–57	0–12.5	12.5–30	30–60	0–12.5	12.5–40	40–60
Mechanical analysis (%):												
Coarse sand	47.3	48.0 ‡	33.5 ‡	25.1	23.4	25.9	13.3	15.4	17.0	4.4	3.0	5.3
Fine sand	33.4	31.4	25.7	30.7	30.1	30.1	50.2	44.8	44.9	18.6	15.1	15.7
Silt	0.4	11.8	6.4	9.7	6.6	8.4	15.1	13.8	11.0	26.0	12.5	10.9
Clay	19.0	8.9	14.4	34.4	39.9	35.7	21.3	26.1	27.2	50.9	69.3	68.1
pH	6.9	6.6	6.4	6.7	6.5	6.6	5.6	4.9	4.9	5.4	6.0	6.3
Exchangeable Ca (mg. equiv. per 100 g. soil)	8.5	3.6	.	2.5	1.9	2.1	5.1	1.7	1.1	9.0	6.2	7.2
Clay analysis:												
SiO_2 (%)	47.2	.	.	45.7	.	.	52.5	.	.	52.1	.	.
Al_2O_3 (%)	35.9	.	.	38.9	.	.	36.5	.	.	39.9	.	.
Fe_2O_3 (%)	10.6	.	.	12.7	.	.	10.5	.	.	6.3	.	.
SiO_2/R_2O_3 (mol. ratio)	1.88	.	.	1.65	.	.	2.06	.	.	2.01	.	.
SiO_2/Al_2O_3 (mol. ratio)	2.23	.	.	1.99	.	.	2.44	.	.	2.22	.	.
SiO_2/Fe_2O_3 (mol. ratio)	11.86	.	.	9.55	.	.	13.30	.	.	22.01	.	.
Al_2O_3/Fe_2O_3 (mol. ratio)	5.32	.	.	4.79	.	.	5.45	.	.	9.92	.	.

‡ Sample, containing a high proportion of pea-iron gravel, which is excluded from the mechanical analysis.

Table 7. *Transect I (Wau); vegetation*

Occurrence in each section is recorded by frequency letters (key on p. 41), or by number of individuals where few. Approximate heights in feet, where noted, are given in brackets (1 ft. = 0·3 m.).

Species In approximate order of progression down the transect and of importance within sections (p. 41)	Habit (Key to symbols p. 41)	Section I Ironstone woodland (E soil phases)	Section II *Combretum* (Col/C and Col/F1 soils)	Section III Transition (Col-II soil)	Section IV *Terminalia* (II/Dr1 soil)	Section V Valley grassland (II/Dr2-II/Id3 soil)
Prosopis africana	CTS	f, ld (1–50)	—	—	—	—
Angeissus schimperi	CT	o, lcd (30–50)	—	—	—	—
Khaya senegalensis	CT	r, ld (20–60)	—	—	—	—
Daniellia oliveri	CT	r, ld (30–60)	—	—	—	—
Burkea africana	CT	r, lcd (40–50)	—	—	—	—
Afrormosia laxiflora	CT	r, lcd (30–50)	—	—	—	—
Parkia oliveri	CTS	r, lcd (2–50)	—	—	—	—
Terminalia mollis	T	o (20–30)	—	—	—	—
Lannea schimperi	T	r (20–30)	—	—	—	—
Strychnos innocua	TS	f, lsd (1–30)	—	—	—	—
Croesopteryx febrifuga	TS	f (5–25)	—	—	—	—
Acacia campylacantha	TS	f (1–20)	—	—	—	—
Dalbergia melanoxylon	TS	r (5–25)	—	—	—	—
Manilkara schweinfurthii	TS	l (10–30)	—	—	—	—
Hexalobus monopetalus	TS	l (5–20)	—	—	—	—
Teclea nobilis	TS	l (10–20)	—	—	—	—
Tamarindus indica	T	r (20–30)	—	—	—	—
Boscia salicifolia	T	l (25)	—	—	—	—
Landolphia senegalensis var. *glabriflora*	TL	l (20–30)	—	—	—	—
Hippocratea richardiana	TL	l (20–30)	—	—	—	—
Hymenocardia acida	TS	f, ld§ (5–15)	—	—	—	—
Rhus natalensis	S	lf (3–8)	—	—	—	—
Strychnos spinosa	TS	l (1–15)	—	—	—	—
Popowia djurensis	S	l (6)	—	—	—	—
Parinari curatellifolia	S (T)	l (seedling)	—	—	—	—
Hyparrhenia sp. HS 45 (indet.)	G]	a	—	—	—	—
Andropogon gayanus	G]		—	—	—	—
Ctenium elegans	G	f, la†	—	—	—	—
Hyparrhenia barteri var. *calvescens*	G	o, la†	—	—	—	—

Species						
Bulbostylis coleotricha	G	la†	—	—	—	—
Sporobolus sp. HS 42 (indet.)	G	lf†	—	—	—	—
Indigofera bracteolata	Us	lf†	—	—	—	—
Lepidagathis sp. aff. *fischeri*	Us	lf†	—	—	—	—
Hyparrhenia sp. HS 44 (annual, indet.)	G	r	—	—	—	—
Cymbopogon giganteus	G	l	—	—	—	—
Pterocarpus abyssinicus	CT	r (30–45)	r (20–45)	—	—	—
Vitex doniana	CTS	r, ld (20–40)	l (1–40)	—	—	—
Diospyros mespiliformis	TS	r, ld (3–30)	o (1–2)	—	—	—
Lonchocarpus laxiflorus	TS	l (25)	r (6)	—	—	—
Butyrospermum parkii var. *niloticum*	TS	o, ld (10–30)	l (6)	—	—	—
Combretum verticillatum	S	lf (2–8)	f (1–6)	—	—	—
Bauhinia thonningii	S (T)	o (6–8)	l (5)	—	—	—
Gardenia lutea	S	r (6)	r (4)	—	—	—
Ziziphus abyssinica	TS	r (5–15)	l–} (3–8) l*	—	—	—
Pavetta schweinfurthii	S	r (2–3)	l (2)	—	—	—
Combretum ghasalense	TS	—	a (1–20)	—	—	—
Ficus capensis	T	—	lf (15–20)	—	—	—
Entada sudanica	T	—	l (15–20)	—	—	—
Combretum binderanum	T	—	l (20)	—	—	—
Lannea schweinfurthii	S (T)	—	l*	—	—	—
Gymnosporia senegalensis	S (T)	—	l (3–8)	—	—	—
Crateva adansonii	S (T)	—	l* (3)	—	—	—
Cochlospermum tinctorium	Us	—	lf	—	—	—
Hibiscus sabdariffa	H	—	o	—	—	—
Grewia mollis	S (T)	a, lsd (5–10)	lf (10)	lf (4–6)	—	—
Bridelia scleroneuroides	TS	lf (1–15)	o (3–10)	l (5–7)	—	—
Mitragyna inermis	CT	—	—	ld‡ (30–50)	—	—
Terminalia glaucescens (?)	T	—	—	lf (15–20)	—	—
Albizzia zygia	S (T)	—	—	l (½–6)	—	—
Sarcocephalus esculentus	S (T)	—	—	lf (5–8)	o	—
Terminalia laxiflora	TS	—	—	o (3)	f, ld (25–35)	—
Ziziphus mauritiana	S (T)	—	—	—	l*	—
Hyparrhenia rufa	G	—	la	ld (10)	d	d (6½)

§ This species was locally dominant where pea-iron was showing on the surface.

* On or beside termite mounds (Col/F1+, Il/Dr1+).

† In pockets of soil or cracks between bare ironstone in a small area of E/O phase.

‡ A group of eight *Mitragyna* trees on the margin of a water-hole—a localized Il/Id2 site.

Exchangeable calcium

The figures for all the sections show the effect of vegetation in increasing the exchangeable calcium in the surface horizon. The clear example of this in the E/Dp soil of section I could be ascribed to the relatively dense vegetation, with termite activity in addition; but the same feature is also shown very clearly in section IV. In section II, where the exchangeable calcium is very low, the horizon difference is not so marked. The relatively high content of exchangeable calcium found at all depths in section V is of course to be expected, even in the quite acid surface horizon, because of the large amount of clay present.

Clay analysis

The silica content is higher in sections IV and V (Il) than in sections I and II (E and Col), suggesting that some resilication of the clay has occurred on the illuvial sites. The figures for ferric oxide are fairly high (10–13 %) in sections I, II and IV, and markedly lower (6 %) in section V. It may be that in section IV (Il/Dr 1) the immersion by an oscillating flood is such as to cause alternate oxidation and reduction of iron but not to remove it, since the iron content of the clay is not noticeably diminished compared with the flood-free sections above. In section V, on the other hand, with a longer period of immersion, more complete reduction occurs and larger amounts of iron are finally removed in the drainage water.

The SiO_2/Al_2O_3 ratio does not vary greatly, nor does it indicate a high degree of eluviation. But when the iron is included (SiO_2/R_2O_3), a difference is shown between sections I and II, in which the ratio is below 2, and sections IV and V, in which it is above 2. The clay of section II (Col/F 1) shows the lowest ratio, which suggests that on this site the material has undergone more complete weathering than on the eluvial complex. This relation, which is in part paralleled in the other transects, may prove to be an important character of colluvial as compared with eluvial soils.

The SiO_2/Fe_2O_3 ratio appears to indicate more clearly the difference between the clays on these sites. If the ratio for the eluvial soil of section I be considered to represent the normal for the climate, there seems to be retention of iron in the colluvial section II to a degree not easy to explain, although it may be due to the relative absence of reducing conditions on the slope. This is followed in section IV (Il/Dr 1) by a slight reduction in the iron content, contributing to a higher ratio, and this becomes still more marked in section V (Il/Dr 2-Il/Id 3). The difference between section I and section IV is due to a larger amount of silica in the clay complex in section IV, whereas the difference between section IV and section V is due to a smaller amount of iron in section V. The former difference results from resilication and the latter from the removal of ferrous iron. Since both of these causes of a higher ratio are promoted by 'low-level' drainage conditions, it is suggested that the SiO_2/Fe_2O_3 ratio and the iron content of the clay may together prove valuable in the characterization of the different members of a soil catena, although it should be remembered that the present figures take no account of the coarser constituents.

VEGETATION RECORDS, TRANSECT I

Table 7 (p. 46), recording the vegetation of the Wau transect, and the preceding description of the vegetation by sections, require little discussion, since this transect represents the simplest expression seen of the E-Col-Il catena. Attention may, however,

be drawn to the two most striking floristic features of the catena brought out by Table 7 and shown in a more compact and elegant form in this transect than in those described later. In the first place, the species show a marked 'drift' from the upper to the lower sections, expressing the essential differences in the specific components of the three complexes, E, Col and Il. In the list of sixty-two species, only two woody species, both always of very general occurrence (*Grewia mollis* and *Bridelia scleroneuroides*) and only one of the few identifiable herbaceous species (the grass *Hyparrhenia rufa*) show a distribution wider than two adjacent sections. Secondly, the E complex has by far the richest flora, at any rate as seen at a season when the herbaceous component is largely withered or burnt. The greater area surveyed for section I does not vitiate this statement, whose truth is self-evident in the region at large.

The analysis which follows, of a less damaged tract of eluvial woodland, resolves the E mosaic into some of its components.

ELUVIAL MOSAIC NEAR TRANSECT I; TERMITE MOUNDS

Date: 2 February 1939.
Location: About 6 km. (4 miles) north-east of Wau; on the north-west side of the Wau-Meshra road, about 1·5 km. (1 mile) from it along the branch road leading to Nyin Akok.
Area examined: About 270 × 270 m. (300 × 300 yd.).
Slope: None perceptible.

The area formed part of a comparatively unspoilt stretch of high-level woodland on a flat ridge-top, continuous with the ridge on which section I of Transect I was located and only 2–3 km. (1–2 miles) from the latter. Mr W. E. Marshall, the Forest Officer stationed at Nyin Akok, stated that the woodland had not been burnt for two years—an exceptional circumstance in a region where annual burning is almost ubiquitous. The area was for the most part covered by woodland of varying density (phases E/Dp+, E/Dp, E/S), but on the south-west side there was a wide, treeless band of E/S.R phase, whose vegetation was very largely burnt.

The woodland as a whole was open (E/Dp and E/S phases), but it contained many dense patches with much evergreen undergrowth. The densest of these were on and around termite mounds in various stages of development and decay (E/Dp+ phase), while others covered patches of deeper soil not obviously of termite origin. With the object of finding whether there was any demonstrable relation between the stage of decay of termite mounds and the characteristics of their soil and vegetation, soil samples were taken from four mounds, and the vegetation on and closely surrounding each of them was fully listed. Three of the mounds (A, B and C) were more or less definite, conical or low elevations showing obvious termite origin, and apparently in three stages of subsequent disintegration. The fourth (D) was a widespread, slight elevation apparently derived from a termite mound long since completely collapsed. Obliteration of all effects of a former mound involves, however, not only the above-ground portion, but also the underground channels. According to Troll (1936) the material composing large mounds may be brought up from a depth of 7–8 m. (23–26 ft.). Penetration to any such depth, unless by single shafts (Marais, 1939), hardly seems probable on ironstone sites, but it is clearly necessary to bear in mind the possibility of persistent underground effects after all surface traces have gone.

For comparison with the four mound samples, the soil of a rather shallow E/Dp site,

in the open woodland near mound D, was also sampled. The vegetation of the open woodland was listed near each of the mound sites in turn, the resulting lists being combined as a record covering E/Dp and E/S vegetation jointly. Finally, the soil of the treeless area (E/S.R) was sampled; of its mostly burnt vegetation little remained to examine.

The general aspect of the area is well shown by Phot. 12. The dominant trees of the woodland, of which the most important were *Khaya* (evergreen) and *Anogeissus* (deciduous), occurred mainly, but not only, in the dense patches. *Khaya* often emerged above all other species, the largest specimens occurring in the dense patches, especially in those which included a termite mound. The open parts of the woodland were chiefly composed of small trees and shrubs of the subsidiary species, which formed a mixed, locally continuous scrub; in many places this was overtopped by a mixture of the deciduous co-dominants, forming closed or open canopy, and in other places by single trees, mostly *Lannea* and *Butyrospermum*. There was a complete ground-cover of medium-tall grass and herbs, dense where not shaded.

DESCRIPTION OF SITES
Termite-mound sites (E/Dp+)

Mound A

A conical mound 1·5 m. (5 ft.) high and about the same in diameter at the base, whence the surface sloped gradually away to the surrounding level ground which was about 0·3 m. (1 ft.) lower. There was evidence that the upper part of the mound, at least, was of very recent origin, although inspection of this part revealed no definite sign of present termite occupation.

Soil. E/Dp+ phase. Two parts of the mound were sampled.

(i) Sample from the interior of the summit of the mound: Pale pinkish red (R. pl. XIV Cinnamon rufous), sandy clay, slightly micaceous, very compact and cemented, containing galleries and fine pin-hole channels; a very little fine pea-iron.

(ii) A hole was dug in the lower part of the side of the mound, at a point about 30 cm. (12 in.) above the surrounding level ground.

0–2·5 cm. (0–1 in.). Pale brownish red (R. pl. XXIX Mikado brown), sandy clay, with finely vesicular structure; a little very fine pea-iron.

2·5–20 cm. (1–8 in.). Paler brownish red (R. pl. XXIX Mikado brown, soil slightly redder), sandy clay; finer in texture, more compact and less vesicular than above; pea-iron as above.

Vegetation. Dominated by three deciduous *Anogeissus* 6–15 m. (20–50 ft.), one *Tamarindus* and one *Boscia salicifolia* both 12 m. (40 ft.) high. The two latter, though retaining most of their leaves in the dry season, cast only light shade. The evergreen shrubs beneath were unusually small, and of these only two species occurred on the steep, conical part of the mound. The remaining subordinate trees and shrubs, mainly two or three species of *Combretum*, with numerous herbs and woody seedlings (*Strychnos* sp., etc.), occurred in a ring on and around the lower slope of the mound. Three facts support the view that the conical part of this mound was a recent, secondary erection on a previously collapsed mound, and that the subordinate members of the community were developing on a disturbed site: (i) the small size and numbers of the evergreen shrubs, especially on the conical part of the mound; (ii) the fact that the bases of the large trees were partially covered by the mound; (iii) the occurrence, on this mound only, of the two adventive species *Grewia mollis* and *Bridelia scleroneuroides*.

Mound B

About 1 m. (3 ft.) high, apparently considerably older than mound A, more extensive in area and of low, convex outline.

Soil. E/Dp+ phase. 2·5 cm. (1 in.) layer of dead leaves on the surface.

0–2·5 cm. (0–1 in.). Brownish red (R. pl. XXIX Verona brown) loam, loose and friable, with vesicular structure; a very little fine pea-iron.

Phot. 12. Eluvial mosaic near Transect 1. Two large *Khaya senegalensis* trees dominating a dense ever-green patch on a termite mound (E/Dp); tall, open woodland in background on E/Dp, with out-standing *Khaya*; smaller trees and shrubs in front of this on E/S; treeless E/S.R area in foreground, with burnt grasses and herbs (cf. Phot. 13) and mushroom-shaped termite mounds.

Phot. 13. Eluvial mosaic near Transect 1; to left of Phot. 12. Dense growth on 'mound B' (E/Dp), showing co-dominant *Anogeissus* (A) and *Tamarindus* (B), with spreading, evergreen *Maba* beneath. Foreground (E/S.R) as in Phot. 12 but unburnt; the ironstone blocks mark a small outcrop (E/O).

2·5–25 cm. (1–10 in.). Pale brownish red (R. pl. XXIX Mikado brown), heavy loam, compact and becoming more so with depth, somewhat vesicular; a little fine pea-iron.

Vegetation (Phot. 13, background). Considerably denser and more shady than that of mound A. Dominated by two large *Tamarindus* 15 m. (50 ft.), two smaller *Khaya* 11 m. (35 ft.) and three *Anogeissus* 9 m. (30 ft.) high, with three semi-evergreen lianes (*Opilia*) attaining 11 m. The subsidiary evergreen trees and shrubs were well grown, and many were rooted on the raised part of the mound, notably a spreading *Maba* 4·5 m. (15 ft.) high. Only the three dominant trees and one typical shade-tolerant evergreen (*Strychnos innocua*) occurred as established members of the community on this mound and also in the open woodland away from mounds. The species abundant in the herb layer on the mound proper were typical shade-tolerants, not adventives. The general impression gained was of a more mature community than that on mound A.

Mound C

Evidently an old mound, now nearly flat, some 7–9 m. (8–10 yd.) in diameter at the bottom and rising at the centre only 0·3–0·6 m. (1–2 ft.) above the surrounding level ground.

Soil. E/Dp+ phase. 5 cm. (2 in.) layer of dead leaves on the surface.

0–5 cm. (0–2 in.). Reddish brown (R. pl. XXIX Snuff brown) loam, loose, with vesicular and crumb structure; a very little fine pea-iron.

5–30 cm. (2–12 in.). Pale reddish brown (R. pl. XXIX Mikado brown), heavy loam, more compact and somewhat redder than above, with vesicular structure; a little fine pea-iron, increasing at 60 cm. (2 ft.).

Vegetation. Dominated by one *Anogeissus* 15 m. (50 ft.) and one *Tamarindus* 9 m. (30 ft.) high, casting only a moderate shade on the rather open growth of subsidiary evergreen trees and shrubs, none of which had attained more than 4·5 m. (15 ft.); small herbs and woody seedlings were numerous all round. The aspect and composition of the small community was in all essentials similar to that of mound A, though perhaps somewhat more stabilized, in that it lacked the more obviously adventive species.

Mound D

A slightly elevated and widely spreading site, selected as a typical example of the islands of dense vegetation on comparatively deep soil which, though probably of termite origin, now bear no superficial signs of termite building. This site seems to show some relationship with mounds A, B and C in both soil analysis and floristics, and forms an interesting and probably significant intermediate in both these respects between the definite mounds and the open wood.

Soil. E/Dp+ phase. 7·5 cm. (3 in.) layer of dead leaves on the surface.

0–5 cm. (0–2 in.). Brown (R. pl. XXIX Snuff brown, soil somewhat darker), sandy loam, slightly micaceous, loose and friable, with vesicular and crumb structure; some large and small pea-iron.

5–25 cm. (2–10 in.). Brownish red (R. pl. XXIX Mikado brown) loam, mixed with quartz fragments and a great quantity of large and small pea-iron of darker colour (R. pl. XXIX Warm sepia).

Vegetation. Dominated by two large trees of evergreen *Khaya* 15 m. (50 ft.) and 21 m. (70 ft.), and one *Anogeissus* 15 m. (50 ft.) high. Below these a dense thicket was formed by subsidiary evergreen and deciduous shrubs and trees up to 12 m. (40 ft.) high, together with three lianes and numerous saplings of two *Combretum* spp. (leafless and unidentifiable). The shade cast by the canopy was comparable with that on mound B, but except for the dominant *Khaya* there is no closer floristic relationship with mound B than with A and C. The general aspect was that of a relatively mature and stable community.

Open woodland sites

E/Dp phase

The soil was examined on a site, near mound D, representing the denser parts of the open woodland. Blocks of ironstone lay scattered on the surface. The darker colour of the soil compared with that of the mounds is probably due to admixture of ash, derived from the burning of the grass. This is much more plentiful in the open wood and, until recently, had almost certainly been burnt every year.

Soil. 6 cm. (2·5 in.) layer of dead leaves on the surface.

0–7·5 cm. (0–3 in.). Purplish brown (R. pl. XXIX Bister), loamy, fine sand, loose and friable, with vesicular and crumb structure; some large and small pea-iron and a few irregular-shaped ironstone concretions.

7·5–30 cm. (3–12 in.). Reddish brown (R. pl. XXIX Snuff brown) loam, mixed with a great quantity of large and small pea-iron and irregular ironstone concretions darker in colour (R. pl. XXIX Warm sepia) than the soil; soil becoming redder and more compact with depth and passing into red ironstone.

Vegetation. Dominated, on such comparatively deep sites, by a mixture of deciduous, leguminous trees (*Pterocarpus, Burkea, Afrormosia, Parkia, Amblygonocarpus*) with occasional *Anogeissus.* These together formed a canopy of variable density at 12–15 m. (40–50 ft.). Below these were smaller deciduous trees and shrubs and a moderately dense layer of medium-tall perennial grass, with herbs and woody saplings locally frequent. A notable feature of this particular woodland, as compared with others in the neighbourhood, was the frequency of *Khaya* saplings of all sizes from 1·5 to 6 m. (5–20 ft.).

E/S phase

On another site, in a more open part of the woodland, the soil was mixed with pea-iron from the surface to 18 cm. (7 in.); at this depth there were larger aggregates of ironstone 3–5 cm. (1–2 in.) across. The vegetation in this more open part was mostly dominated by the smaller trees (notably Combretums) and shrubs, with emergent single trees such as *Lannea schimperi* and *Butyrospermum* at intervals. Here the grass, perennial and annual, was considerably denser, mixed in many places with thorny scrub, locally dense, of *Strychnos spinosa, Acacia campylacantha* and *Ziziphus abyssinica*, with *Hymenocardia* locally frequent.

Treeless area (E/S.R)

An elongated area, approximately 185 m. (200 yd.) wide, extending for a considerable distance beside the woodland examined. The foregrounds of Phots. 12 and 13 show typical parts of the area. Mushroom-shaped termite mounds about 30 cm. (1 ft.) high were abundant. Outcrops of ironstone occurred in several places, and scattered blocks of ironstone were locally numerous. A few slightly raised, mound-like patches of deeper soil, probably collapsed large termite mounds, bore trees and shrubs in groups which appeared to be residual.

Soil. E/S.R phase. A pit was dug on ground with deeper soil than the average for the treeless area. It was close to an exposed surface of massive ironstone forming slightly higher ground, and probably represents a pocket in which the shallow soil eroded from the ironstone had accumulated. The horizons were as follows:

0–15 cm. (0–6 in.). Pale brown (R. pl. XXIX Sepia, soil somewhat paler), loamy, fine sand, loose and friable with vesicular and crumb structure; a little fine pea-iron.

15–20 cm. (6–8 in.). Pale yellowish brown (R. pl. XXIX Saccardo's umber, soil somewhat paler), mixed with much pea-iron (mostly fine), irregular ironstone concretions and larger, hard aggregates of ironstone 3–5 cm. (1–2 in.) across.

A level, open site near this showed a higher proportion of pea-iron in the soil, and an irregular ironstone surface appeared at 15 cm. (6 in.).

Vegetation. Where not burnt, dominated by a mixture of annual grasses 30–60 cm. (1–2 ft.) high, including *Ctenium elegans*, with various annual and perennial herbs. Perennial grasses and the under-shrub *Barleria grandicalyx* were scattered and locally frequent as spaced tufts, burnt over most of the area.

SOIL ANALYSIS, ELUVIAL MOSAIC

The data are given in Table 8.

Termite-mound sites

The four mound soils form an interesting series. In gross structure the samples from the base of mound A and from the older mounds B, C and D, have every appearance of resulting from gradual disintegration of the termite-built structure shown by the sample from the summit of A, the newest mound.

Mechanical analysis

The clay content shows a maximum (60%) in the sample (i) from the galleried interior of the summit of mound A. Near the base of the same mound the proportion of clay is very high (roughly 50%) in both horizons, the surface approaching double the figure for mounds B and C. It seems that as the mounds age, this fine material is washed out, especially near the surface, until in the oldest mound (D) the amount of clay near the surface is only about 15%, although this is still over double the low proportion (6%) in the E/Dp soil of the surrounding open woodland. Mound D was similar in appearance to the sites used for cultivation by the Jur tribe who inhabit the high-level woodlands in this part of the country, and the amount of clay in excess of the E/Dp quantity is probably in itself sufficient to account for the selection of such sites for this purpose; increased base status, however, may also contribute to their productivity.

Table 8. *Eluvial mosaic near Transect I; soil analysis*

	Mound A†			Mound B		Mound C		Mound D		Open woodland (E/Dp)		Treeless area (E/S.R)	
	(i)	(ii)											
Cm. from surface ...	—	0–2·5	2·5–20	0–2·5	2·5–25	0–5	5–30	0–5	5–25	0–7·5	7·5–30	0–15	15–20
Mechanical analysis (%) ...	.	.	.	.	.	.	.	.	‡	.	‡	.	‡
Coarse sand	8·0	10·0	8·5	14·9	12·1	17·2	15·9	28·8	21·5	39·6	36·1	61·9	64·8
Fine sand	21·4	32·1	26·0	39·5	35·5	48·0	36·2	41·4	30·9	33·4	31·9	24·4	21·9
Silt	10·8	9·7	7·5	18·3	15·4	9·1	10·6	14·9	10·5	20·8	12·6	7·8	5·8
Clay	59·8	48·2	58·0	27·3	37·0	25·7	37·3	14·9	37·1	6·2	19·4	5·9	7·5
pH	7·5	6·7	6·3	7·4	7·5	7·5	7·6	6·0	5·4	6·5	5·5	6·1	5·6

(Newest)←Termite-mound sites→(Oldest) (E/Dp+)

† (i) Sample from the interior of the summit of the mound.

(ii) Two samples from a hole dug in the lower part of the side of the mound, at a point about 30 cm. (12 in.) above the surrounding level ground.

‡ Sample containing a high proportion of pea-iron gravel, which is excluded from the mechanical analysis.

pH *values*

In general, the pH figures show a tendency to alkalinity in the E/Dp+ termite-mound soils as compared with the acidity of the E/Dp and E/S.R soils.

The oldest mound, D, has an acid reaction similar to that of the normal E/Dp woodland soil, and it seems reasonable to suppose that old mounds such as D must undergo leaching during a long period of gradual collapse.

Mounds B and C have pH values practically identical with that of the interior of the summit of mound A, the reaction in each case being slightly alkaline. The base of mound A, on the other hand, is appreciably acid. This difference, suggesting a longer duration of leaching, would result if the base of A were not only an older construction than its present conical summit, as suspected on other grounds (p. 50), but also older than mounds B and C. It must be noticed, however, that the respective clay contents (A summit > A base > B and C) do not suggest, as the pH values do, that the base of A is the oldest of these four soils.

These inconclusive arguments are worth bringing forward because they show something of the complex soil problem involved in the ageing of termite mounds—a problem

Table 9. *Eluvial mosaic near Transect I; vegetation*

Occurrence on each site is recorded by frequency letters (key on p. 41), or by numbers of individuals where few. Approximate heights in feet, where noted, are given in brackets (1 ft. = 0·3 m.).

Species in approximate order of progression: newest mound→oldest mound→shallow soil	Habit (key to symbols p. 41)	Termite-mound sites (E/Dp+ soil) (Newest)←⎯⎯→(Oldest)				Open woodland (E/Dp and E/S soils)	Treeless area (E/S.R soil)
		Mound A	Mound B	Mound C	Mound D		
Boscia salicifolia	CT	1‡ (40)	—	—	—	—	—
Grewia mollis†	S	o (5)	—	—	—	—	—
Capparis sp. (indet.)	S (Cl)	1‡	—	—	—	—	—
Opilia celtidifolia	TL	1 (2)	3‡ (to 35)	—	—	—	—
Diospyros mespiliformis	TS	1 (3)	2‡ (4), 3 (6–15)	2 (4–10)	—	—	—
Rhus natalensis	S	1 (5)	3 (10)	1 (10)	—	—	—
Boscia senegalensis	S	2‡ (1–2)	1‡ (3)	1 (5) (spreading widely)	—	—	—
Wissadula amplissima var. *rostrata*	H	a	a	a (1–4)	—	—	—
Sansevieria sp. HS 182 (indet.)	H	o‡ (5)	a‡	1f	—	—	—
Ximenia americana	TS	1 (5)	1	1 (15)	—	—	—
Adenia venenata	ClS	—	1‡ (15)	1	—	—	—
Maba abyssinica	TS	1 (‡)	3 (to 10)	2 (1–2)	1 (1)	—	—
Popowia djurensis	S	f‡ (1–5)	a‡	5 (2–5)	a (to 12)	—	—
Teclea nobilis	S (T)	—	1‡ (4)	—	1 (2)	—	—
Manilkara schweinfurthii	TS	—	—	1 (8)	4 (12–40)	—	—
Landolphia owariensis var. *tomentella*	TL	—	—	—	2 (20)	—	—
Canthium malaccocarpum	TL	—	—	—	1 (20)	—	—
Pavetta schweinfurthii	Us	—	—	—	1 (3)	—	—
Anogeissus schimperi	CT	3‡ (20–50)	3‡ (30)	1 (50)	1 (50)	o (to 40)	—
Hexalobus monopetalus	TS	3 (3)	1 (2)	1 (2)	3 (5–30), f (seedlings)	o, lf	—

Tamarindus indica	CT	1‡ (40)	2‡ (50)	1 (30)	—	r	—
Gardenia lutea†	S	2 (1)	—	1 (1)	—	o (to 8)	—
Combretum lecananthum†	TS	a (6–15)	—	—	—	f	—
C. ghasalense†	TS	1 (20)	—	—	—	lf	—
Bridelia scleroneuroides†	S	1 (8)	—	—	—	r	—
Khaya senegalensis	CTS	—	2 (35)	—	2 (50–70)	o, lf (5–20)	—
Strychnos innocua	TS	—	1 (15)	—	—	l (to 15)	—
Pterocarpus abyssinicus	CT	—	—	—	2 (15–20)	o, lcd	—
Croesopteryx febrifuga	TS	—	—	—	1 (20)	o	—
Strychnos spinosa	TS	—	—	—	1 (15)	o, lf	—
Burkea africana	CT	—	—	—	—	r, lcd	—
Afrormosia laxiflora	CT	—	—	—	—	r, lcd	—
Parkia oliveri	CT	—	—	—	—	r, lcd	—
Amblygonocarpus schweinfurthii	CT	—	—	—	—	r, lcd (to 50)	—
Ficus sp. (indet.)	T	—	—	—	—	r, lcd	—
Lannea schimperi	T	—	—	—	—	o, ld	—
Lonchocarpus laxiflorus	T	—	—	—	—	—	—
Butyrospermum parkii var. *niloticum*	TS	—	—	—	—	r, ld (to 40)	—
Acacia campylacantha	TS	—	—	—	—	o (to 5)	—
Hymenocardia acida	S(T)	—	—	—	—	lf	—
Ziziphus abyssinica	S	—	—	—	—	o	—
Combretum verticillatum	G	—	—	—	—	l	—
Hyparrhenia barteri var. *calvescens*	G	—	—	—	—	a, ld (2–3)	—
Labiate herb (indet.)	H	—	—	—	—	a, ld (2–3)	—
Sporobolus sp. (*festivus* ?)	G	—	—	—	—	la	a, lcd
Ctenium elegans	G	—	—	—	—	—	a, lcd
Other annual and perennial grasses and herbs	G, H	—	—	—	—	—	—
Barleria grandicalyx	Us	—	—	—	—	—	la

† Occurrence of these species (adventives etc.) explained on pp. 56–7.

‡ Occurrence on the mounds proper; the remaining species occur in a ring round the edge.

likely to be solved only by a study of mounds in considerable numbers. The present mechanical analysis and pH figures, from only a few samples, at least provide some confirmation of the changes which are usually considered to be brought about by termite activity. Several comparable instances might be cited of basic conditions localized in termite mounds, sometimes in a fashion much more marked than that recorded here; Burtt (1942, p. 125), for instance, found free carbonate in mounds erected on acid soil; Thomas (1943), as mentioned earlier, gives other relevant references. One of these is to Milne's report, now made generally available, which suggests interesting lines of inquiry into this phenomenon (Milne, 1947, p. 233).

Open woodland and treeless area

Mechanical analysis

The soils of the two level sites, E/Dp and E/S.R, are both decidedly coarser than the mound soils. The E/Dp surface soil from the open woodland, compared with the corresponding soil from Transect I, section I, contains considerably less clay and more silt, a difference explicable by the termite activity already mentioned (p. 44) as probably concerned on the Transect I, E/Dp site. There is at the same time a pronounced difference between both of these E/Dp woodland soils and the E/S.R soil of the treeless area, involving a lower proportion of fine fractions in the latter, but most readily seen in its much higher proportion of coarse sand. It seems clear that from the E/S.R site, which may be liable to sheet erosion, much of the finer portion of the soil has been removed.

pH *values*

The soils of both sites, E/Dp and E/S.R, are rather more acid in their surface horizons, and considerably more so below, than the E/Dp soil from Transect I. The surface soil of the treeless area (E/S.R) is more acid than that of the neighbouring as well as the more distant (Transect I) E/Dp woodland site. This difference would support the generally held view that a less acid surface on eluvial sites is maintained by the leaf fall of denser vegetation.

THE INFLUENCE OF TERMITE MOUNDS AND OF FIRE ON THE ELUVIAL WOODLAND VEGETATION

Table 9 (p. 54), arranged to bring out the 'drift' in floristic composition from the definite termite-mound sites A, B and C, through the very low mound D, to the open wood, clearly shows a group of species with a preference for the three definite mound sites. This preference cannot be attributed to shade alone; mounds B and D, which have in common a much heavier shade than A and C, show no special floristic similarity, for they share exclusively between them only two species—*Khaya* which casts most of the shade, and *Teclea* with one small plant on each site.

The intermediate floristic status of mound D, between the three less degenerate mounds and the open wood, would be more elegantly shown in Table 9 but for the interpolation, half-way down, of four species whose local distribution is known to be peculiar in the present connexion. These four are: *Combretum lecananthum*, which was often observed forming a ring of saplings and small trees around, but not on, termite-mound sites, thus qualifying for its record in the open woodland rather than on mounds; *Gardenia lutea* and *Combretum ghasalense*, which occur widely scattered on nearly all phases in ironstone

woodland; and *Bridelia scleroneuroides*, which (with *Grewia mollis*) has already been mentioned as adventive on any well-drained site. The interruption of the tabulated drift of species by these four may therefore be explained as 'accidental' through their known peculiarities.

It is in any case apparent from Table 9 that the totally collapsed mound D has a flora substantially distinct from that held, in the main jointly, by the three less degenerate mounds A, B and C; furthermore, mound D showed appreciable growth of only one species (*Popowia djurensis*) considered from general observation to be specially characteristic of mounds. The inference is that many of the characteristic species disappear after the mound collapses. This inference may also be drawn from the fact that mounds in general do have a characteristic flora not found in the rest of the woodland, which can be presumed to contain sites of obliterated mounds—most probably where the denser vegetation grows.

The presence of a defined group of species on the termite mounds may be due to one or more of the following influences:

(i) The soil of the mounds, with a higher clay content than the surrounding E/Dp soil, retains more moisture in the dry season, when dampness is perceptible even by touch. In high-level woodland this factor seems likely to be much more important than any quicker surface drainage which may occur during the rains. In a discussion of these problems quoted by Hegh (1922), Becquaert took the contrasting view that termite mounds are essentially drier habitats than the surrounding savanna woodland. This opinion evidently refers to woodland broadly resembling our area, and is not concerned with the types of mound which are devoid of plant growth. It is derived from Becquaert's interpretation of the evergreen and (more plausibly) the sometimes succulent habit of characteristic mound species as an indication of xerophytism. The issue is complicated by the fact, amongst others, that different parts of mounds probably differ widely in dampness. It may, indeed, be true that the higher parts of steep mounds are dry. That the lower parts, exploited by the roots of the chief plants, are damp can only be proved by moisture determinations; meantime, however, there seems every reason to believe that they are in the present instance.

(ii) Whether or not they owe their initial establishment to relatively good soil moisture, most of the species keep their leaves green and apparently functional throughout the dry season, when the surrounding vegetation is almost leafless. The resulting shade practically eliminates grass and therefore fire. The combined effects of shade and freedom from fire would naturally tend to perpetuate a shade-tolerant, evergreen community.

(iii) With some of the species the preference for mounds may have a chemical basis, the soil pH and, we may provisionally assume, the base status being higher in the mounds than in the surrounding level ground.

(iv) The species characteristic of mounds may be free from termite attack. Certainly no case can be recalled of any of them showing signs of consumption by termites, while such signs were frequently seen on several of the species characteristic of the open woodland.

(v) It is quite a striking fact that most of the termite-mound species have fruits which are likely to be eaten by birds roosting on the branches of the larger trees such as *Khaya*. As a cause of observed species-distribution, however, such a means of dispersal fails to tally with the absence of most of the fleshy-fruited species from mound D, which was

dominated by two very large *Khaya* trees. Further, the complete absence from the open woodland of nearly all the species with small, fleshy fruits can hardly be ascribed merely to a concentration of seed-dropping by birds in the denser patches of vegetation; and by the same token the preponderance in the open woodland of leguminous trees which do not seem to require bird-dispersal of their seeds, seems adequately explained by the physiological adaptability of the tree Leguminosae.

Consideration of these potential causes of a characteristic termite-mound flora leaves a first impression that the edaphic properties of the mounds exercise, more or less directly, the supreme influence. It cannot be assumed, however, that all of the mound species owe their characteristic occurrence in the same habitat to identical factors. The precise relation between the vegetation of termite-mound soils and that of the surrounding shallower soil phases requires much more intensive and thorough investigation, especially from the dynamic standpoint. Vegetational succession on such soils, which may be complicated by the production of new termite mounds on the top of moribund ones (originally built by the same or perhaps a different species of termite), can be adequately studied only by workers with facilities for continued observation and a knowledge of termites as well as of soils and vegetation. The preliminary data and tentative conclusions given here are sufficient to show that more detailed analysis would be repaid by instructive results.

The respite from burning, which enabled a relatively close study of this area of woodland through reducing its defacement by fire, also brought forth some early indications of the profound effects of regular burning. The most striking features observed on this area, unburnt for two years, as compared with the ordinary burnt woodland of the same neighbourhood, were the more plentiful leaf litter and the numerous saplings of *Khaya* in the open woodland. *Khaya* saplings were practically never seen in the average burnt woodland except in the dense patches (normally around termite mounds), and their successful growth to 6 m. (20 ft.) in this recently unburnt area suggests that, with another year or two free from burning, many of them would be sufficiently robust to withstand an occasional fire running through the grass at their base. If they reached sufficient size to shade out most of the inflammable herb layer, fires would automatically be less frequent and less fierce. On E/Dp and especially E/S soil, *Khaya* and other trees might well never attain the good growth shown on E/Dp+ sites, but their contribution to the value of the woodland as a whole and the improvement of its soil would presumably be very great. The indications seen on this area, that developments such as those just described might follow prolonged freedom from burning, seem sufficient endorsement of the policy of fire-protection advocated in the government Soil Conservation Committee's report (Sudan Government, 1944; p. 41, Minute 65; p. 72, para. (v); pp. 143–4, Appendix XXIII).

TRANSECT II (HALIMA CATENA-VARIANT)

Date: 5 February 1939.

Location: About 25 km. (15 miles) south-west of Wau; here, on the north bank of the river Busseri near its confluence with the Halima stream, lie a government saw-mill and the Halima (Ngowlima) Rest House; about 1·6 km. (1 mile) north-west of this point is a ridge and beyond it a fairly wide valley; these formed the site of Transect II.

Slope: Almost level in section I, about 1 in 5 in section II. The relative slopes of the remaining sections III–IX are shown in Fig. 3. Section IX was on the edge of a channel eroding back into sections VIII and VII and having no apparent outlet at the lower end.

Aspect: Approximately north-west.
Length: About 400 m. (440 yd.).
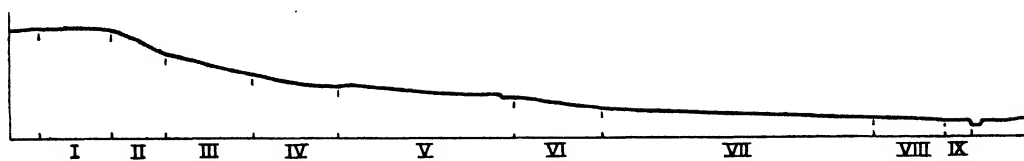Width: Average 22 m. (25 yd.).
Vertical rise: 25–30 m. (80–100 ft.).

Fig. 3. Approximate profile of Transect II. The slope is exaggerated. The sections are numbered.

This transect consists of two catenas; sections I–IV pass from extensive E woodland to Col/F 1; sections V–IX, following the same line, extend from a narrow, secondary E ridge through well-marked Col phases to ground of poorly developed Il character. This sequence is explained more fully below (p. 66).

<div align="center">DESCRIPTION OF SECTIONS</div>

Section I

Ironstone woodland (Phot. 14). Top of upper catena.

Length 37 m. (40 yd.). Roughly level ridge-top. Many loose boulders and fixed blocks of ironstone; large and small patches of soil between them. Surface uneven; no obvious termite mounds, but some of the larger patches of soil were slightly raised and may have been of termite origin.

Soil. Shallow E soil washed into pockets between ironstone blocks; separate E phases not differentiated (except for exposed E/O ironstone).

0–7·5 cm. (0–3 in.). Brown (R. pl. XXXIX Hays brown), sandy, containing much pea-iron, and blackened by admixture of ash.

7·5 cm. (3 in.) —. Hard, yellow-red ironstone.

Vegetation. Deciduous woodland, almost leafless at this season, with a considerable sprinkling of evergreen trees averaging about 25% of individuals. General canopy 6–11 m. (20–35 ft.) high, with an occasional tree attaining 12 m. (40 ft.). No old trees present. Canopy dense in places but mostly open, with many smaller trees and shrubs, especially *Hymenocardia*, which was abundant in the open parts. Occasional lichens were noticed on trees and boulders. These were not seen on Transect I, and probably indicate a somewhat higher rainfall. The area had been cut over for timber; this probably explains the low canopy.

Section II

Scrub-woodland with *Hymenocardia* (Phot. 16).

Length 28 m. (30 yd.). Erosion slope, about 1 in 5. Ironstone boulders smaller and more scattered than in section I.

Soil. E/S-E/S.Er phase, on eroded edge of the eluvial ridge.

0–10 cm. (0–4 in.). Pinkish brown (R. pl. XXIX Vinaceous cinnamon), sandy, with much pea-iron.

10 cm. (4 in.) —. Hard ironstone.

Vegetation. Trees and shrubs widely spaced and mostly small, up to about 4·5 m. (15 ft.) high; one mixed group of *Isoberlinia* (in leaf) and *Burkea*, up to 12 m. (40 ft.) high, forming closed canopy locally, with associated shade-loving species. A notable feature was the abundance in the shrub layer of *Hymenocardia*, the characteristic plant of E/S.Er soils.

Section III

Isoberlinia woodland (Phot. 17).

Length 45 m. (50 yd.). Gently undulating, crossed obliquely by the line of the transect.

Soil. E-Col transition.

0–17·5 cm. (0–7 in.). Pinkish brown (R. pl. XXIX Vinaceous cinnamon), sandy, with a little pea-iron of various sizes.

17·5 cm. (7 in.) —. Soft, slightly moist ironstone.

Vegetation. An open association with *Isoberlinia* (in leaf) as the chief species and several other medium-sized and small deciduous trees and several shrubs. The *Isoberlinia*, 11 m. (35 ft.) high, was gregariously dominant over part of the area, in places forming a closed canopy below which were a few shade-loving species.

Section IV

Combretum scrub (Phot. 18).

Length 45 m. (50 yd.). More level than section III, and without boulders.

Soil. Col/F 1 phase (but much shallower than the well-developed form shown in section VII). Surface cracked into slightly up-rolled flakes, as though covered by filamentous algae when wet.

0–7·5 cm. (0–3 in.). Pinkish brown (R. pl. XXIX Cinnamon), sandy loam with a little pea-iron.

7·5–20 cm. (3–8 in.). Brown (R. pl. XXIX Vinaceous cinnamon), with more and slightly larger pea-iron.

20 cm. (8 in.) —. Hard, red ironstone.

Vegetation. An open association of small trees of *Combretum* spp., with a few shrubs; three dead trees of *Terminalia* sp. (probably *T. mollis*), apparently killed by fire. Sparse tufts of perennial grass, burnt. This upper *Combretum* zone is scarcely a typical one, and is much inferior in development to the lower example forming section VII.

Section V

Hymenocardia (Phot. 19). Top of lower catena.

Length 90 m. (100 yd.). Slope gentle and mostly smooth, with occasional small termite mounds. An outcrop of ironstone occurred on a local steeper slope near the lower edge of the section.

Soil. E/S.Er phase.

0–10 cm. (0–4 in.). Almost entirely composed of pea-iron gravel with a small amount of pale brown (R. pl. XL Wood brown), sandy loam.

10–25 cm. (4–10 in.). Pinkish brown (R. pl. XL Fawn colour) mixture of soil and smaller pea-iron.

Vegetation. A thicket of *Hymenocardia* 3–4·5 m. (10–15 ft.) high, with other associated shrubs and scattered deciduous trees. Surface of ground covered with ash from an evidently thorough burn, the only herbaceous growth left being remnants of one species of annual grass noted locally. Near the lower edge of the section a small patch of bamboo (*Oxytenanthera*) was associated with a local outcrop of ironstone.

Section VI

Butyrospermum (Phots. 20 and 21, right).

Length 45 m. (50 yd.). Slight slope. Surface smooth except for grass tufts and occasional small termite mounds containing pea-iron.

Soil. Col/C phase.

0–7·5 cm. (0–3 in.). Dark brown (R. pl. XLVI Drab), fine sand, loose and porous, with a little pea-iron.

7·5–20 cm. (3–8 in.). Redder (R. pl. XL Avellaneous), loose and porous, with considerably more fine pea-iron.

20 cm. (8 in.) —. Hard and compact, with red and yellow mottling, suggesting an ironstone in process of development.

Vegetation. Woody vegetation very sparse and localized, for the most part apparently burnt out altogether, either intentionally or accidentally. An irregular group of eight trees of *Butyrospermum* near the lower edge of the section, otherwise only scattered small trees and shrubs and remains of grass and herbs, the dominant perennial grass being apparently *Andropogon gayanus*.

Phot. 15. Part of same ridge-top as Transect II, section I. Bare ironstone outcrop (E O phase); under-shrubs, grasses and herbs in cracks. Mixed evergreen and deciduous woodland behind on shallow E soil.

Phot. 14. Transect II (Halima), section I. Light-barked *Hymenocardia* among blocks of ironstone, and large-leaved *Isoberlinia* and *Afzelia*, in mixed woodland on shallow E soil.

Phot. 16. Transect II (Halima), section II. Looking down the erosion slope (E S-E S.Er phase) into a dense patch of *Isoberlinia* and *Burkea*.

Phot. 17. Transect II (Halima), section III. Dominant *Isoberlinia* on the E-Col transition phase.

Phot. 18 Transect II (Halima), section IV. *Combretum* (foreground, in leaf) preponderant in mixed scrub-woodland on Col/FI phase.

Phot. 19. Transect II (Halima), section V. *Hymenocardia* (A) dominating scrub with *Gardenia* (B) etc., on low, eroded ridge (E/S.Er phase).

Phot. 20. Transect II (Halima), section VI. Looking down through a group of large *Butyrospermum* on Col/C phase, into *Combretum* zone of section VII on Col/F1.

Phot. 21. Transect II (Halima). Right, lower edge of section VI (Col/C phase), with large *Butyrospermum*; left, upper edge of section VII (Col/F I), with dense *Combretum*.

Phot. 22. Transect II (Halima), section VII. *Combretum* on Col/F I phase.

Phot. 23. Transect II (Halima), section VII. *Oxytenanthera* (bamboo) on Col F2 phase.
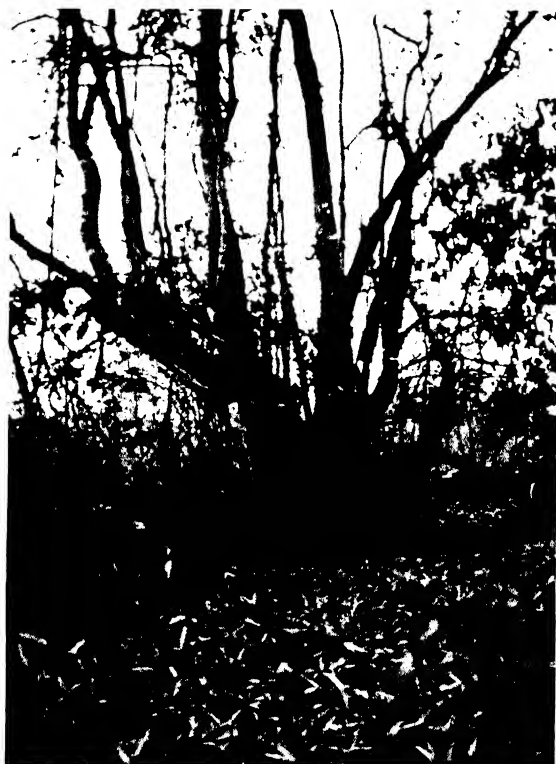
Phot. 24. Transect II (Halima), part of section IX. *Mitragyna* on edge of dry drainage channel bordered by mixed II phases.

Phot. 25. Transect III (Aweil), part of section I. *Sclerocarya* (A) on E/Dp phase; dark *Khaya senegalensis* behind it in dense evergreen patch on E/Dp ; foreground (E/S.R) bare after burning of annual grasses and herbs.

Phot. 26. Transect III (Aweil), section II. Low *Combretum* (A) and shrubs on Col/F1 phase around soil-pit; large *Khaya senegalensis* dominating dense patch on a mound (Col/F1).

Section VII

Combretum (Phot. 22).

Length 140 m. (150 yd.). Slight slope. Surface smooth except for grass tufts and occasional termite mounds.

Soil. Col/F 1 phase.

0–7·5 cm. (0–3 in.). Brown (R. pl. XLVI Drab), friable, fine sand, loose and porous, with traces of fine pea-iron.

7·5–20 cm. (3–8 in.). Pale brown (R. pl. XLVI Drab), sandy, less porous and more compact, with traces of pea-iron.

20–30 cm. (8–12 in.). Reddish brown (R. pl. XLVI Drab, soil somewhat yellower), with traces of fine pea-iron.

30 cm. (12 in.) —. Brown (R. pl. XXIX Pinkish buff), with many reddish spots and streaks of iron staining.

Vegetation. Begins abruptly as a dense grove of young trees of *Combretum*, mostly 4·5–8 m. (15–25 ft.) high, with occasional other species of trees and shrubs. Dense grass in tufts, generally burnt off but remaining in places. A few herbs and undershrubs left after burning.

Section VIII

Bamboo brake (Phot. 23).

Length 37 m. (40 yd.). Almost level. Surface smooth except for grass tufts.

Soil. Col/F 2 phase.

0–20 cm. (0–8 in.). Chocolate brown (R. pl. XLVI Hair brown), heavy loam, friable and loose.

20–40 cm. (8–16 in.). Chocolate brown, somewhat pinker (R. pl. XLVI Hair brown); fine texture and clod structure, with brown streaks and iron staining.

Vegetation. Dominated by large clumps of bamboo (*Oxytenanthera*) 3–8 m. (10–25 ft.) high, with a few rather large trees and scattered shrubs, and fairly dense grass in tufts.

Section IX

Mixed 'low-level' vegetation ('*Mitragyna* mixed').

A frontage of 55 m. (60 yd.) along the edge of a short, dried-up, muddy channel with no apparent outlet at the lower end, eroding back into sections VIII and VII.

Soil. Mixed Il phases (Il/Dr 1, Il/Id 1–2), but the sample, taken from the bed of the dried-up channel, was more characteristic of Il/Id 3. Surface sample only.

Grey (R. pl. LI Mouse grey) with much iron mottling; hard, compact and deeply cracked, with a little transported pea-iron.

Vegetation. A fairly well defined belt of trees, medium to large for the locality, on and near the edge of the dried-up channel. The only frequent species *Mitragyna* (Phot. 24), the remainder represented mainly by one tree of each species. A few shrubs and remains of grasses and herbs.

SOIL ANALYSIS, TRANSECT II

The data are given in Table 10 (p. 62).

The bi-catenary nature of this transect, arising from the interrupted nature of the topography, is discussed below in connexion with the vegetation (p. 66). Sections I–IV form the upper and sections V–IX the lower catena. Two phases, E/S.Er and Col/F 1, are represented, though in differing form, in both catenas. Otherwise the extended lower catena has a character and phase-representation distinct from those of the mainly steep upper catena.

Table 10. *Transect II (Halima); soil analysis*

	Section I	Section II	Section III	Section IV		Section V		Section VI		Section VII				Section VIII		Section IX
Soil phase ...	E soil of ridge top	E/S–E/S.Er	E-Col	Col/F1		E/S.Er		Col/C		Col/F1				Col/F2		II/Id2–3
Vegetation type ...	Ironstone woodland	Scrub-woodland with *Hymenocardia*	*Isoberlinia*	*Combretum* scrub		*Hymeno-cardia*		*Butyro-spermum*		*Combretum*				Bamboo		'*Mitragyna* mixed'
Cm. from surface ...	0–7·5	0–10	0–17·5	0–7·5	7·5–20	0–10	10–25	0–7·5	7·5–20	0–7·5	7·5–20	20–30	30–	0–20	20–40	0–7·5
Mechanical analysis (%):		‡				‡	‡									
Coarse sand	59·6	50·0	46·3	31·7	35·6	47·7	40·9	32·5	33·8	25·3	26·5	21·3	24·4	10·8	4·5	12·2
Fine sand	31·7	30·6	42·7	50·6	45·9	40·1	41·5	55·4	45·8	56·9	55·3	48·3	44·7	42·8	40·2	20·7
Silt	4·4	8·1	3·9	6·0	5·1	4·4	4·6	6·6	8·4	9·3	6·8	11·4	13·0	21·3	23·3	19·2
Clay	4·2	11·3	7·2	11·6	13·4	7·8	13·0	5·5	12·0	8·4	11·4	18·9	17·8	25·1	31·9	47·8
pH	6·4	6·6	6·3	6·0	4·4	5·4	4·8	6·3	5·6	6·1	6·4	6·7	6·8	5·4	5·2	5·4
Clay analysis:																
SiO_2 (%)	45·0	·	46·8	40·1	·	·	·	45·8	·	48·9	·	·	·	45·4	·	50·2
Al_2O_3 (%)	42·7	·	38·6	37·9	·	·	·	35·1	·	36·9	·	·	·	36·4	·	32·4
Fe_2O_3 (%)	9·6	·	14·6	14·1	·	·	·	12·3	·	11·1	·	·	·	11·5	·	9·9
SiO_2/R_2O_3 (mol. ratio)	1·56	·	1·66	1·45	·	·	·	1·80	·	1·89	·	·	·	1·76	·	2·20
SiO_2/Al_2O_3 (mol. ratio)	1·79	·	2·06	1·80	·	·	·	2·21	·	2·25	·	·	·	2·12	·	2·63
SiO_2/Fe_2O_3 (mol. ratio)	12·46	·	8·54	7·58	·	·	·	9·86	·	11·68	·	·	·	10·51	·	13·53
Al_2O_3/Fe_2O_3 (mol. ratio)	6·97	·	4·16	4·22	·	·	·	4·46	·	5·19	·	·	·	4·97	·	5·15

‡ Sample containing a high proportion of pea-iron gravel, which is excluded from the mechanical analysis.

Upper catena

This consists of the eluvial complex and a rather ill-defined colluvial slope.

Mechanical analysis

The soils of sections I and II contain large amounts of pea-iron, excluded from the analysis. Comparing these two soils, the lower (II) contains more fine material. As between sections III and IV, the lower soil is again the finer. On examining the four soils, pea-iron included, there is an obvious increase downhill in fineness of texture.

pH *values*

These are normal and of the same order as in Transect I. It is notable that in the poorly developed Col/F1 zone (section IV) acidity increases markedly with depth, contrasting with the much greater uniformity of pH through the horizons in the fully developed Col/F1 of section VII.

Clay analysis

Comparing the figures with the corresponding ones from Transect I, the lower ratios for SiO_2/R_2O_3 and SiO_2/Al_2O_3 in the present transect indicate greater laterization, which could well be attributed to the rather higher rainfall. As in Transect I, the Col/F1 zone shows a value for SiO_2/R_2O_3 which is appreciably less than that of the ground above it whence its material comes. The E-Col figure, however, does not show this relation to the eluvial summit; much fuller data are of course needed before these relations can be further discussed.

Lower catena

The lower catena consists of a much-eroded eluvial phase, followed by an extended colluvial slope and an illuvial belt which is too narrow for differentiation into separate phases.

Mechanical analysis

In its analysis-fractions the soil of section V (E/S.Er) is akin to the E soils of the upper catena; its resemblance is all the greater because, like sections I and II, it contains a large amount of pea-iron. From section VI (Col/C) downhill there is a marked increase in the clay content, which reaches the high figure of 48% at the surface in section IX.

pH *values*

Again these call for little comment, except that the increase of acidity with depth in sections V (E/S.Er) and VI (Col/C) contrasts with a decrease with depth in section VII (Col/F1), where some drainage impedance was indicated in the lowest horizon. Samples from the lower horizons of sections IX would, with little doubt, have shown decreasing acidity.

Clay analysis

The highest silica content on the transect is in the illuvial section IX, whose value of 50·2% resembles those for the illuvial sections IV and V in Transect I. The clay-component ratios, considered in turn, show distinct similarity in the three colluvial sections (VI, VII, VIII), and they also resemble those for the colluvial soil in Transect I; but they are not

Table 11. *Transect II (Halima); vegetation*

Occurrence in each section is recorded by frequency letters (key on p. 41), or by number of individuals where few. Approximate heights in feet, where noted, are given in brackets (1 ft. = 0·3 m.).

Species mainly in approximate order of progression down the transect (p. 66)	Habit (key to symbols p. 41)	Upper catena				Lower catena				
		Section I Ironstone woodland (E soil)	Section II Scrub-woodland with *Hymenocardia* (E/S-E/S.Er soil)	Section III *Isoberlinia* (E-Col soil)	Section IV *Combretum* scrub (Col/F1 soil)	Section V *Hymenocardia* (E/S.Er soil)	Section VI *Butyrospermum* (Col/C soil)	Section VII *Combretum* (Col/F1 soil)	Section VIII Bamboo (Col/F2 soil)	Section IX '*Mitragyna* mixed' (II/Dr-II/Id1-2 soil)
Daniellia oliveri	CT	3 (35)	—	—	—	—	—	—	—	—
Afzelia africana	CT	2 (15–35)	—	—	—	—	—	—	—	—
Khaya senegalensis	CT	1 (40)	—	—	—	—	—	—	—	—
Parinari curatellifolia	TS	3 (2–30)	—	—	—	—	—	—	—	—
Maba abyssinica	T	1 (20)	—	—	—	—	—	—	—	—
Londolphia petersiana var. *schweinfurthiana*	TL	2 (35)	—	—	—	—	—	—	—	—
Hippocratea richardiana	TL	1 (35)	—	—	—	—	—	—	—	—
Popowia djurensis	S	1f (10)	—	—	—	—	—	—	—	—
Teclea nobilis	S (T)	1 (10)	—	—	—	—	—	—	—	1
Boscia senegalensis	S	1	—	—	—	—	—	—	—	1* (15)
Cadaba farinosa	S	1	—	—	—	—	—	—	—	1
Detarium senegalense	TS	3 (15–20)	r (1–15)	—	—	—	—	—	—	—
Maerua schweinfurthii	T	2 (30)	1 (20)	—	—	—	—	—	—	—
Lannea schimperi	CT	2 (20–35)	1 (15)	—	—	—	—	—	—	—
Randia nilotica	T	1 (20)	1 (15)	—	—	—	—	—	—	—
Tamarindus indica	T	1 (15)	1* (15)	—	—	—	—	—	—	1* (40)
Burkea africana	CTS	3 (1–40)	lcd (30–40)	—	—	o (1–25)	1 (15)	—	—	—
Prosopis africana	CTS	1 (35)	3 (10–15)	—	—	1 (25)	1	—	—	—
Hymenocardia acida	TS	a (5–15)	3 (5–15)	—	—	d (10–15)	—	—	—	—
Crossopteryx febrifuga	TS	a (5–15)	a (7–15)	—	—	o	—	—	—	—
Butyrospermum parkii var. *niloticum*	TS	—	2 (2–15)	—	—	r	ld (15–35)	—	—	—
Combretum spp. A, B and C (indet.)	TS	—	lsd*	—	—	—	1	—	—	—
Grewia mollis	S (T)	—	lf	—	—	—	—	lf	o	—
Vitex madiensis	T	—	1 (15)	—	—	—	—	—	—	—
Courbonia virgata	Uᴮ	—	la* (1–2)	—	—	—	—	—	—	—
Ziziphus abyssinica	S (T)	—	1 (2)	—	—	—	—	—	—	—
Ochna sp. (indet.)	S	—	1 (1)	—	—	—	—	—	—	—
Strychnos spinosa	S (T)	—	1 (1)	—	—	f	—	—	—	—
Diospyros mespiliformis	TS	2 (5–25)	1* (6)	1 (10)	—	—	—	—	—	1 (10)

Species	Habit	1	2	3	4	5	6	7	8
Rhus natalensis	S	1 (10)	—	1 (5)	1	—	—	—	—
Strychnos innocua	TS	f (15–20)	f	a, lsd	—	—	—	—	—
Isoberlinia doka	CTS	2 (25–30)	lcd (30–40)	a, ld (35)	—	—	—	—	—
Anogeissus schimperi	CT	1 (35)	1* (25)	o (30–45)	—	—	d (1–25)	1 (40)	3 (30–40)
Combretum verticillatum	S	—	1	ld	—	—	lf	—	—
Boscia salicifolia	T	—	—	1 (20)	o	—	r	—	—
Vitex doniana	T	—	—	1 (20)	—	—	—	—	—
Combretum ghasalense	T	—	—	1 (20)	—	—	—	—	—
Bridelia scleroneuroides	S (T)	1 (6)	—	0 (3)	—	—	—	—	—
B. micrantha	S (T)	2 (2)	1* (10)	1	—	—	—	—	—
Annona senegalensis	S (T)	—	—	1	r	2	—	—	—
Ximenia americana	S (T)	—	—	1	r	—	—	—	1 (10)
Gardenia aqualla	S (T)	—	—	lf	1	—	—	—	—
Combretum undulatum	TS	—	2 (2)	1	—	—	—	—	—
Terminalia mollis	TS	3 (10–15)	—	lf	3 (10–20)	3 (10–15)	1f	r	—
Combretum glutinosum	TS	—	—	o (15)	—	1	r	—	—
Gymnosporia senegalensis	S (T)	—	—	1	r	r	—	—	—
Urginea sp. (*indica?*)	H	—	—	r	—	—	—	—	—
Lepidagathis appendiculata	Us	—	—	1	o	—	—	—	—
Gardenia erubescens	S	—	—	—	r	1	—	—	—
Ctenium elegans	G	—	—	—	1	1	—	—	—
Combretum sp. D (indet.)	S (T)	—	—	—	—	r	—	—	—
Gnidia kraussiana	H	—	—	—	—	d	r	—	—
Andropogon sp. (*gayanus ?*)	G	—	—	—	—	—	a	—	—
Combretum sp. E (indet.)	T	—	—	—	—	—	1 (25)	—	—
Pterocarpus abyssinicus	T	—	—	—	—	—	1 (30)	—	—
Cissus cornifolia	S (Cl)	—	—	—	—	—	o	—	—
Anthericum sp. HS 191 (indet.)	H	—	—	—	—	—	o	—	—
Indigofera hendecaphylla	Us	—	—	—	—	—	1	—	—
Bauhinia thonningii	S (T)	—	—	—	—	—	o	r (5)	—
Acacia seyal var. *multijuga*	S (T)	—	—	—	—	—	o	d (10–25)	—
Oxytenanthera abyssinica	TS	—	—	—	—	—	—	3 (25)	—
Terminalia sp. (indet.)	T	—	—	—	r, 1	—	—	1 (35)	—
Sterculia setigera	T	—	—	—	—	—	—	—	—
Justicia betonicoides	H	—	—	—	—	—	—	r	—
Rhynchosia caribaea	H	—	—	—	—	—	—	2	—
Mitragyna inermis	CTS	—	—	—	—	—	—	—	1f (5–50)
Pseudocedrela kotschyi	CT	—	—	—	—	—	—	—	1 (20)
Kigelia aethiopica	CT	—	—	—	—	—	—	—	1 (20)
Carissa edulis	S	—	—	—	—	—	—	—	1 (4)
Jussiaea suffruticosa	Us	—	—	—	—	—	—	—	1

* Termite-mound occurrences; those in section II on the site of a derelict mound which locally reduced the otherwise steep slope; those in section IX on a small mound probably of termite origin.

matched in the feebly developed Col/F 1 soil of section IV. The contrast between sections VI–VIII (Col) and section IX (Il) depends not only on a larger silica content in section IX, but also on a smaller amount of both alumina and ferric oxide. Thus section IX, although representing a rather ill-defined illuvial complex, shows its illuvial character by a silica/sesquioxide ratio which is high as compared with the colluvial phases; the other two transects show the same relationship.

Vegetation records, Transect II

Elucidation of this transect in terms of the usual catena sequence depends upon the recognition here of two catenas which at first sight appeared to occupy a single topographical gradient. In fact, however, the gradient is broken, as shown in Fig. 3 (p. 59), at the top of section V, which is also marked by an outcrop of ironstone in its lower part. Although this section is a shorter distance from the valley bottom than is the evidently colluvial section IV, its eluvial character is unquestionable, the soil and vegetation being of the distinctive E/S.Er type observed in many places including (as a modified example) section II of this transect. Section V therefore represents the top of a second catena.

The sequence of phases in the two catenas thus recognized is conveniently shown by the column headings in Table 11 (p. 64). It will be noticed that two phases—E/S.Er (in a partial degree) and Col/F 1—are each represented twice. The floristic repetition involved becomes evident with Table 11 constructed as follows. The species occurring in sections I–IV are arranged according to their occurrence in these four sections only, without reference to their occurrence in the lower sections; their occurrence in sections V–IX is then added; the names of the species which occurred only in sections V–IX follow, their order based on occurrence in the usual way. It will be noticed that the 'drift' of occurrence shows a fresh start with the renewed appearance in section V of six species recorded in section II, but not in sections III and IV. This could only happen if there were a distinct floristic relationship between sections V and II, and this relationship is confirmed by the fact that section II contains all the more important and characteristic species of section V. While the two eluvial sections of the upper and lower catenas thus show a marked similarity in floristic content, the two Col/F 1 sections (IV and VII) do not produce a similar effect in the table. This is largely because the vegetation of each contained, as its chief element, a single species, *Combretum undulatum*, with *C. glutinosum* as a further main component in each case. The similarity visible on the site was therefore greater than the general appearance of the table would suggest.

Sections I, II and III are in general aspect very typical of the catena-variant named after Halima and widely found thence westwards and southwards. These three sections, particularly II and III, acquire this vegetational aspect in large measure from the occurrence of *Isoberlinia*, which attains its best development from 150 to 250 km. (90–150 miles) west of Wau, on abrupt ridges, and on slopes from ridges and hills consisting of parent gneiss and producing relatively immature soils. Halima, by virtue of its hilly configuration, forms the edge of an eastern outlier of this western district, and shows strong circumstantial evidence of a similarly higher rainfall than the Wau district. The vegetation of Transect II and its immediate neighbourhood includes other trees besides *Isoberlinia* which are characteristically frequent or even gregarious and dominant farther west. This applies to *Afzelia*, *Parinari* and *Detarium*, which here occur in small numbers; *Protea madiensis*, which occurred near this transect, seems to show a similar tendency.

This last, like *Isoberlinia*, is so far as known absent from the Wau catena-variant, including the neighbourhood of Transect I, little more than 25 km. (15 miles) from Halima.

Sections VIII and IX require comment in that they represent features characteristic of the Halima-catena variant as opposed to the other two variants recognized. The valley containing the lower part of the transect was drained by a stream, dry at the time of the investigation but in the wet season probably bringing down eroded material in considerable quantity from nearby hills. Through occasional floods which may overflow this stream, as well as by local surface wash-down, section VIII is likely to accumulate from its hilly surroundings material of a type which is not available in catena-variants in flatter country. At any rate the Col/F 2 phase of section VIII, with its thicket of bamboo (*Oxytenanthera*), conforms to wider observations of the occurrence of this type, to which attention has already been drawn (p. 24).

Section IX represents a narrow, illuvial belt which, apart from the muddy channel, appeared relatively well drained. This narrow belt is too restricted for its flora to be compared with that of any particular recognized illuvial phase or phases. The chief woody species present are *Mitragyna*, characteristic of Il/Id 2, and *Anogeissus* which, apart from termite mounds, particularly frequents Il/Id 1. *Pseudocedrela*, represented here by a single tree, is normally a good indicator of Il/Dr 1 conditions; almost always when observed it was in association with *Terminalia macroptera* on Il/Dr 1 sites.

Despite differences in detail, most of the characteristic species of Transect I, with the notable exception of *Khaya*, are characteristic of the corresponding sections of Transect II. There was another slope, situated only a few hundred metres distant from Transect II, leading down from a similar ridge to a more level and less well-drained part of the valley. Here the sequence of zones characteristic of the Wau catena-variant was closely reproduced. As well as a high-level (E) ironstone top (Phot. 15) and slope, there was a *Combretum* (Col/F 1) zone, a narrow belt of *Terminalia* (Il/Dr 1), a narrow, flat, treeless zone (Il/Dr 2) similar to Transect I, section IV, and a very fine, almost pure stand of *Mitragyna* (Il/Id 2) in the wide, muddy bed of the seasonal stream.

The paucity of records of undershrubs, grasses and herbs on this transect is due to the recent fierce fires, which had consumed practically the whole of the ground vegetation in the locality. This was especially unfortunate because there was reason to expect a greater variety of undershrubs and herbs here than in Transect I.

TRANSECT III (AWEIL CATENA-VARIANT)

Date: 15–24 February 1939.

Location: 5–10 km. (3–6 miles) north-west of Aweil; both sides of the Aweil-Nyamlell road; the greater part, including the lower sections, on the east side.

Slope: Just perceptible in sections II, III and V, imperceptible in sections I, IV and VI–X.

Length: About 5 km. (3 miles).

Width: Average roughly 90 m. (100 yd.); varied according to heterogeneity of vegetation.

Vertical rise: Probably less than 3 m. (10 ft.).

This transect covers the transition from ironstone woodland to the flood-plain grassland (toich) of the R. Lol valley. The terrain on both sides of the road was first extensively reconnoitred. Owing to the very slight general slope, the variations induced by micro-relief have sufficient relative importance to obscure zonation and introduce a partly mosaic pattern. Hence it was not found possible to bring all the types represented into one straight transect in the proper order of descending level. The main area of high-level, ironstone woodland, recorded as section I, was separate from a less typical part, also contributing

to the section I records, which led into the rest of the transect. Sections VII–X were not in line with sections I–VI. Section VI was very extensive, varying in width from 1·5 to 3 km. (1–2 miles), and was studied by means of a sample of typical character.

<div align="center">DESCRIPTION OF SECTIONS</div>

Section I

Ironstone woodland (Phot. 25).

Area studied 185 × 275 m. (200 × 300 yd.). Apparently perfectly level surface except for scattered large and small termite mounds. An ironstone outcrop of variable thickness was visible in places at the edge of this section.

Soil. Two phases were examined.

(i) E/Dp phase under canopy. 1·25 cm. ($\frac{1}{2}$ in.) leaf litter on the surface.

0–27 cm. (0–11 in.). Pale pinkish grey (R. pl. XL Wood brown), sandy, with some pea-iron and quartz fragments.

27–32 cm. (11–13 in.). Similar to above but pinker (R. pl. XL Avellaneous), with much large and small pea-iron.

32–75 cm. (13–30 in.). Pea-iron consolidating into soft ironstone.

(ii) E/S.R phase of treeless area, a few yards from above site.

0–12·5 cm. (0–5 in.). Pale yellowish grey tinged with pink (R. pl. XL Wood brown), sandy, with large reddish sand-grains and small pea-iron.

12·5 cm. (5 in.) —. Hard, red and yellow ironstone with some black spots; many quartz grains and a little cemented pea-iron.

Vegetation. A mosaic of large and small patches of trees, with large open areas destitute of woody cover; general appearance very open. Canopy of wooded parts 9–12 m. (30–40 ft.), with outstanding trees up to 15 m. (50 ft.) or more, but in many places only 8–9 m. (25–30 ft.), with a high proportion of shrubs and small trees. At least 90% of individual trees deciduous; effective shade in the dry season only under occasional trees of the evergreen *Khaya*. Evergreen trees and shrubs largely confined to termite mounds or sites showing signs of termite activity. The rarity of evergreens in the canopy, and the consequent dominance by deciduous species like *Sclerocarya* and *Pterocarpus*, constitute an important difference from the corresponding ironstone woodland near Wau (e.g. Transect I, section I). The open areas (E/S.R) were so thoroughly burnt that few traces remained of what was evidently an almost completely annual vegetation similar to that observed on the E/S.R phase in the neighbourhood of Wau.

Adjacent to the area listed there was a small society of *Hymenocardia acida*. This appeared to be the northern limit of range of the species in this part of Equatoria. It was not observed elsewhere near Aweil, nor in the country northwards to the Bahr el Arab. But it may well range farther north on the higher ground near the western border, and it is reported (Broun & Massey, 1929) from the Nuba Mountains (11° N., 30° E.), beyond the northern confines of Equatoria.

Section II

Combretum (Phot. 26).

Length 140 m. (150 yd.); width about 90 m. (100 yd.). Slope hardly perceptible. Surface of ground very smooth and level except for grass tufts and one or two large, low elevations, probably the remains of termite mounds.

Soil. Col/F1 phase.

0–12·5 cm. (0–5 in.). Purplish grey (R. pl. XLVI Hair brown), sandy, compact, with a few rusty specks and streaks and very little pea-iron.

12·5–32 cm. (5–13 in.). Pale purplish grey (R. pl. XL Wood brown), less sandy, less compact, with more rusty specks and very little pea-iron.

32–50 cm. (13–20 in.). Pale yellowish grey (R. pl. XL Avellaneous), somewhat less sandy, with small quartz fragments, more and larger pea-iron, and increased mottling.

50 cm. (20 in.) —. Purplish grey with rusty iron staining, pea-iron agglomerating into ironstone.
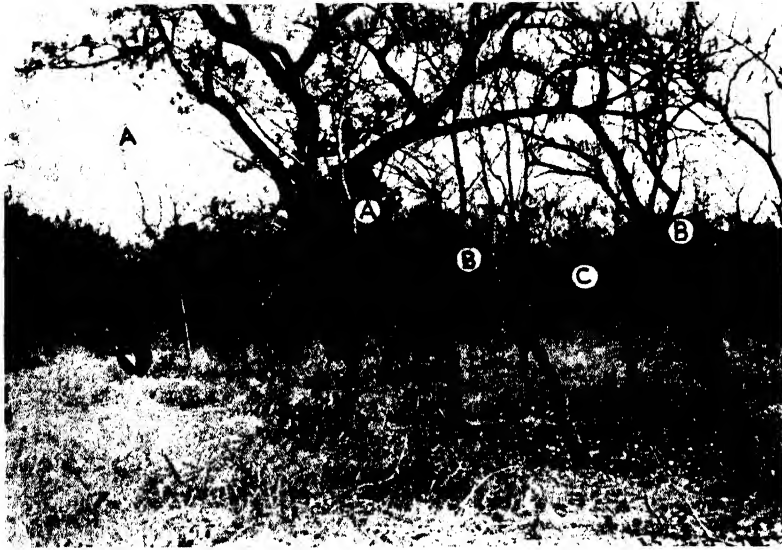
Phot. 27. Transect III (Aweil), section III. *Stereospermum* (A), large spreading *Parkia, Acacia sieberiana* (B), *Entada* (C) and low *Sarcocephalus* amongst grass, all on Col-II transition phase.


Phot. 28. Transect III (Aweil), section IV. *Khaya senegalensis* (A), *Butyrospermum* (B), *Entada* (C) etc. on Col-II transition phase.

Phot. 29. Transect III (Aweil), section VI. *Anogeissus* (A), *Combretum binderanum* (B) and *Balanites* (C) on Il/Id1 phase; group of trees (left) including *Sterculia* (D) and *Lannea schweinfurthii* (E) on Il/Id1 ; a depression in right foreground bears tall perennial grass only.

Phot. 30. Transect III (Aweil); looking into section VII (Il/Id1 phase) from edge of section VIII. *Anogeissus* (A); *Acacia seyal* (B) in a depression; *Gardenia lutea* (C).
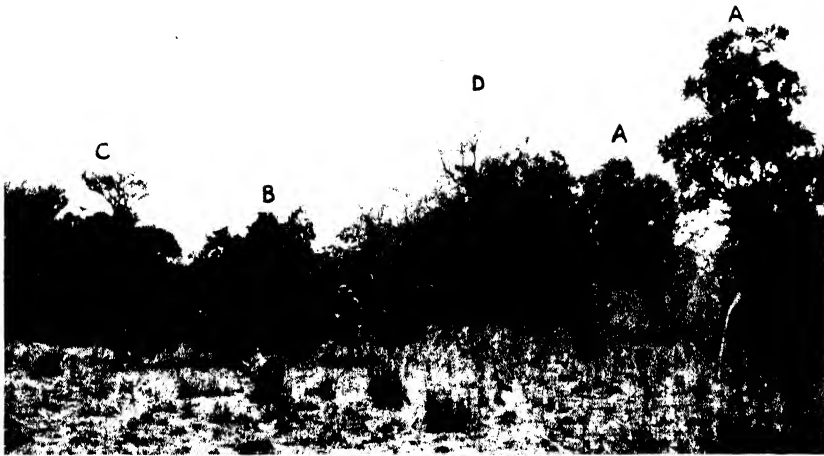
Phot. 31. Transect III (Aweil), upper part of section VIII. Vegetation of various II phases on different levels; *Pseudocedrela* (A) on highest level (II/Dr I); *Bauhinia* (B) in open grass of shallow depression (II/Id2); *Acacia seyal* (C) in partial basin site (II/Id3); *Anogeissus* (D) dominating a dense termite-mound (II/Id2) community.

Phot. 32. Aweil district, near Transect III; a typical stand of *Acacia seyal* on a partial basin site (II/Id3 phase).
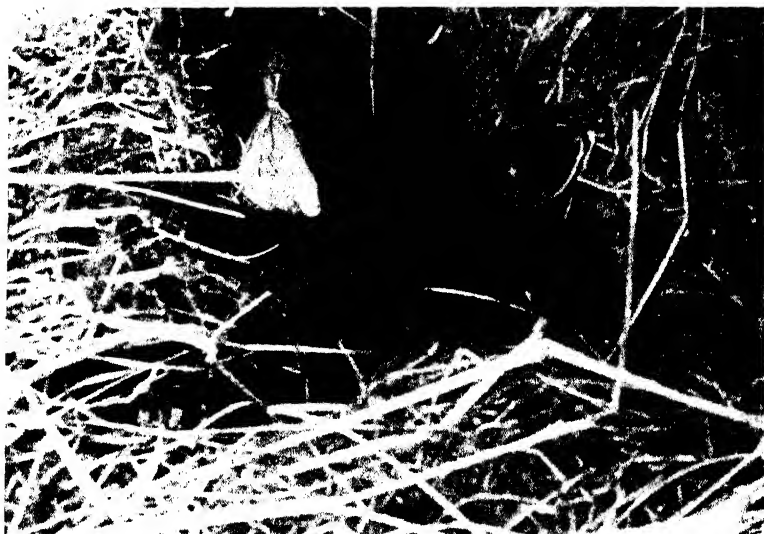
Phot. 33. Transect III (Aweil), section VIII. Looking down into a typical hole ('wong'), as found also in sections V and VI. (See text, p. 30.)

Phot. 34. Transect III (Aweil), upper part of section IX (II/Id2 phase). Vegetation of different levels; *Acacia campylacantha* (A) co-dominant over a termite-mound community on II/Id2 ; *Mitragyna* (B) on intermediate level beside another termite-mound thicket; *Bauhinia* (C) on slight rise in the shallow grassy depression between; the grass is mostly *Vetiveria*.
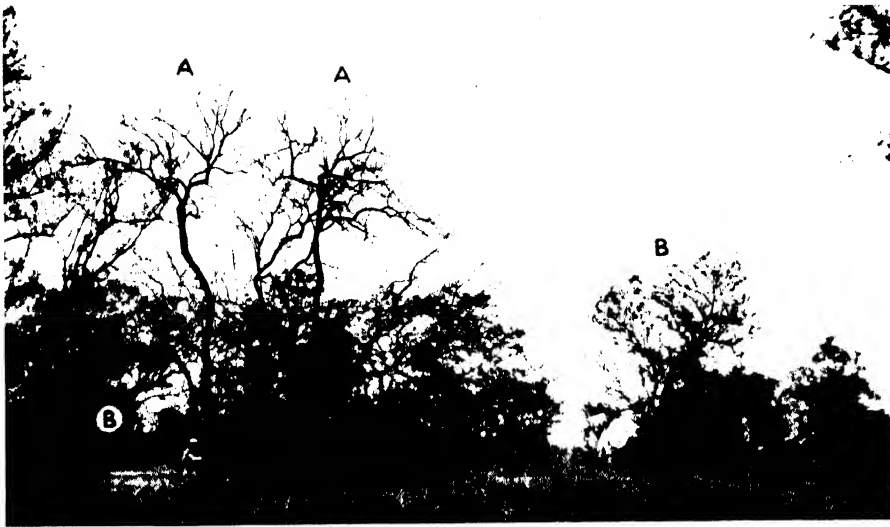
Phot. 35. Transect III (Aweil), middle part of section IX. *Lannea schweinfurthii* (A) etc. on termite mounds (Il/ld2); *Mitragyna* (B) on slightly raised ground in shallow grassy depression (Il/ld2).

Phot. 36. Transect III (Aweil); lower part of section IX, extending into the open grassland of section X. On the horizon are isolated trees of *Mitragyna* on Il/ld2 phase, surrounded by treeless grassland on Il/Dr2; large termite mound dominated by *Diospyros* (A), with *Mitragyna* (B) beside it.

Vegetation. An open association of mostly small trees and shrubs dominated by four species of *Combretum* (in leaf at the time), but with an appreciable contribution by medium to large evergreen *Khaya*—one particularly large, spreading specimen, 15–18 m. (50–60 ft.) high, dominating a dense local association on a low mound. A fairly dense growth of perennial grass, already burnt when seen, included bare patches probably covered in the wet season with annual grass and herbs.

This section and the three next below it contain certain species not characteristic of the phases which these sections primarily represent. The probable explanation is given on p. 74, para. (ii).

Section III

'Entada transition' (Phot. 27).

Length about 185 m. (200 yd.); width about 90 m. (100 yd.). Slope just perceptible. Surface smooth, without grass tufts.

Soil. Col-Il transition.

0–10 cm. (0–4 in.). Dark grey with purplish tinge (R. pl. XLVI Hair brown), compact but with vesicular structure, somewhat less sandy than in section II; signs of seasonal flooding.

10 cm. (4 in.) —. Uniform dark grey (R. pl. XLVI Hair brown, soil somewhat paler), compact.

It is suspected, mainly from vegetational evidence, that this section was cultivated fairly recently, and the appearance of the soil was consistent with this surmise. Its somewhat vesicular structure, as well as its pH (p. 72), would be expected if cultivation included, as it often does, the spreading of soil from termite mounds.

Vegetation. Mostly small trees and shrubs, the stand varying in density in different parts of the area. Little surviving old growth; only one large tree, a *Parkia* 18 m. (60 ft.) high. Signs of destruction of trees and other circumstantial evidence of past cultivation. Surface of ground burnt bare of grass or locally covered by annual plants. No perennial grass tufts observed.

Section IV

'*Combretum-Anogeissus* transition' (Phot. 28).

Length about 185 m. (200 yd.); width about 90 m. (100 yd.). Slope imperceptible. Ground between trees gently undulating; few 'swallow-holes' (p. 30) as compared with section V. Large and small termite mounds frequent. Surface otherwise smooth apart from grass tufts.

Soil. Col-Il transition.

0–12·5 cm. (0–5 in.). Pinkish buff (R. pl. XL Avellaneous), loose, with much coarse sand and some rusty specks.

12·5–32 cm. (5–13 in.). Pale buff (R. pl. XXIX Pinkish buff), compact, sandy, with rusty specks and stains and some small, scattered pea-iron.

Vegetation. Large and small trees of varying density, mostly on large or small elevations often of termite origin, the more level parts of the ground between occupied mainly by tufts of tall perennial grass. Some trees frequent on level ground also, notably *Entada, Combretum* and *Crossopteryx.* Canopy mostly 9–12 m. (30–40 ft.) high, with a few outstanding trees attaining 18 m. (60 ft.). Interesting as showing a transition type between the comparatively well-drained sections II and III, with many trees on level ground, and the undulating sections V and VI, with tree growth almost entirely limited to definite elevations between the seasonally flooded depressions.

Section V

'*Anogeissus* transition'.

Length and width both about 90 m. (100 yd.). Slope just perceptible, but the whole section only very little above the level of section VI. Surface of ground uneven, with alternating depressions and elevations, the latter often of termite origin and some actually surmounted by termite mounds, both large and small. Depressions frequently containing 'swallow-holes' 15–30 cm. (½–1 ft.) across and 30–60 cm. (1–2 ft.) deep.

Soil. Col-Il transition. Not sampled; field notes as follows:

0–12·5 cm. (0–5 in.). Yellowish brown, surface slightly cracked; considerable rusty mottling and scattered, small pea-iron.

Vegetation. About 30% of the area dominated by patches of large and medium-sized trees, nearly all deciduous, with deciduous and evergreen small trees and shrubs beneath; all growing on elevations, most of which appeared to be of termite origin. Canopy of the tree-patches 11–14 m. (35–45 ft.) high, mostly *Anogeissus*, with other associated trees usually smaller. The intervening depressions devoid of woody species except for a few very poorly grown shrubs and regrowth after burning; these species, here in depressions, are in section VIII characteristic of the more elevated parts. Grass of variable height and density under patches of trees, tall and dense in the open.

Section VI

Upper *Anogeissus* (Phot. 29).

Area studied about 185 m. (200 yd.) square. Slope imperceptible, estimated as only 30–60 cm. (1–2 ft.) in 1·6 km. (1 mile). Surface undulating, with large and small raised patches—the majority apparently, and many obviously, of termite origin—and wide, shallow depressions containing frequent 'swallow-holes' 15–60 cm. ($\frac{1}{2}$–2 ft.) across and 30–60 cm. (1–2 ft.) deep.

Soil. Il/Id 1 phase.

0–10 cm. (0–4 in.). Greyish buff (R. pl. XL Buffy brown, soil somewhat lighter), fairly loose, with trace of pea-iron and considerable rusty mottling.

10–30 cm. (4–12 in.). Pale yellowish buff (R. pl. XL Avellaneous), with a little fine pea-iron, and marked iron staining and mottling.

Whitish pebble-sized concretions, presumed to be impure calcium carbonate, occurred close to the surface around termite mounds and on other slight elevations, where in addition the soil surface itself sometimes carried a thin, whitish coating.

Vegetation. Similar to section V, but with patches of trees more definitely confined to mounds or their edges; small trees occurring rarely on slight elevations in the open. Canopy trees practically all deciduous, averaging 11–14 m. (35–45 ft.) high; *Anogeissus* definitely dominant and often attaining 15 m. (50 ft.). Depressions (Il/Id 3) often fringed with *Acacia seyal*, which is also characteristic of the depressions in sections VII and VIII. Grass of variable height and density under tree-patches, tall and dense in the open, about 1·8 m. (6 ft.) high.

Section VII

Lower *Anogeissus* (Phot. 30, background). The lower-lying and denser part of the same woodland type as section VI.

Area studied about 28 × 55 m. (30 × 60 yd.). Slope imperceptible. Surface undulating, with small depressions; the raised parts not obviously of termite origin. 'Swallow-holes' not observed.

Soil. Il/Id 1 phase. Not sampled; field notes as follows:

0–10 cm. (0–4 in.). Grey surface with small cracks; red mottling just below surface; friable, moist.

Vegetation. Dense and almost continuous tree canopy 9–15 m. (30–50 ft.) high, dominated by *Anogeissus*; other deciduous trees occasional, and a fair quantity of semi-evergreen *Balanites* which was typical of the site. Shade appreciable even in the dry season, and a strong tendency to evergreen undershrubs (especially *Boscia senegalensis*) and small evergreen trees. *Anogeissus* saplings a notable feature. Very little grass; several herbs unidentifiable at this season. *Acacia seyal* locally frequent on three sides of the area, grading into section VIII and intrusions of similar ground.

Section VIII

'*Bauhinia*' (Phot. 31).

No precise area. Slope imperceptible. Many large and small termite mounds alternating with shallow depressions of varying extent. The part of the section adjacent to section VII has a very uneven surface with many small, slightly elevated places in and around the depressions, and with many hollows and 'swallow-holes' (Phot. 33). Remainder of the section less undulating, with a more definite contrast between termite mounds and comparatively flat depressions.

Soil. Very variable within short distances, according to micro-relief described above. No careful examination was made of the full range of varying soils. From the nature of the sites and from their

vegetation it was concluded that the following phases were present, with intermediates: Il/Id2, Il/Id2+, Il/Id3, Il/Dr1, and tongues of Il/Dr2 which were really intrusions from section X. An Il/Id2 type of soil was probably the most prevalent.

A sample taken from a local hollow under *Acacia seyal* represents Il/Id3:

0–15 cm. (0–6 in.). Grey-brown (R. pl. XVI Fuscous), fine-textured with surface cracks; copious iron staining within 2·5 cm. (1 in.) of surface.

Elsewhere in the section it was observed that the soil *in situ* had iron staining confined to the lines of root-penetration where oxidation was promoted.

Vegetation. An open, patchy association of very variable composition according to site. Dense groups of trees on termite mounds (Il/Id2+) or other distinct elevations, dominated by deciduous *Anogeissus*, *Acacia sieberiana* and *A. campylacantha*. No woody species in the depressions between, except *Bauhinia* frequently dotted on flat but slightly elevated places (Il/Id2) and *Acacia seyal* gregarious in and around definite local hollows (Il/Id3). Part of section adjacent to section IX more open, with very little *Anogeissus* (which was restricted to termite mounds), much more *Acacia sieberiana*, more *Bauhinia* and *Mitragyna* on elevated parts other than termite mounds, and *Acacia seyal* becoming much less frequent. Open parts throughout dominated by tall grass 1·5–2 m. (5–7 ft.) high (mostly prostrate when seen, probably due to trampling by cattle); in appearance an extension of the open grassland of section X (Il/Dr2), although the connecting portion in section IX bears *Vetiveria*, instead of the *Hyparrhenia* which seems to be the chief grass in sections VIII and X.

Section IX

Mitragyna (Phots. 34, 35).

Of very considerable extent, its ends grading into sections VIII and X. Slope imperceptible, probably only a few inches in several hundred yards. Termite mounds of varying size and height, becoming taller and much fewer towards section X. Elsewhere surface of ground slightly undulating, progressively less so towards section X.

Soil. ll/Id2 phase.

0–10 cm. (0–4 in.). Rather dark brownish grey (R. pl. XLVI Hair brown), compact, with some iron mottling.

10 cm. (4 in.) —. Yellowish grey (R. pl. XL Avellaneous), with much rusty mottling and some transported pea-iron.

Vegetation. Young and mature *Mitragyna* characteristically abundant on slight elevations and on relatively flat ground, but not in depressions; also on and close to termite mounds, though noted as rare on those near section X. All other established trees confined to termite mounds (Il/Id2+) or other definite elevations, in patches up to 12 m. (40 ft.) high, with subsidiary shrubs which, like the trees, are a mixture of deciduous, evergreen and semi-evergreen species. These woody patches decrease in number towards section X. So do the trees and shrubs on intervening ground, *Mitragyna* outdistancing all others as progressively more sparsely scattered trees, finally of rather reduced size, on the slightly elevated tongues extending out into the open grassland of section X. The wide stretches of relatively flat ground, between the tree patches, dominated by tall perennial grass (*Vetiveria nigritana* etc.) up to 2 m. (7 ft.) high, grazed by cattle and much trampled.

Section X

Open grassland (toich).

Several miles in extent. Slope practically nil. Very little lower than section IX. In places undulating very slightly, but most of the surface roughened only by grass tufts.

Soil. Il/Dr2 phase.

0–10 cm. (0–4 in.). Grey-brown (R. pl. XV Warm buff), sandy, loose and dry.

10–30 cm. (4–12 in.). Grey (R. pl. XLVI Light greyish olive), hard and compact, with slight iron mottling.

30–60 cm. (12–24 in.). Grey (R. pl. XLVI Light greyish olive), compact clay with some iron mottling and transported pea-iron.

Vegetation. Grassland of tall, perennial grass in tufts, without woody species. Other herbs probably occur but were not found in the dry season, most of the area having been very thoroughly burnt.

Soil analysis, Transect III

The data are given in Table 12. It should be noticed that the sample from section VIII represents a partial basin site (Il/Id 3) and as such could occur in any of the sections IV to IX.

Mechanical analysis

Compared with corresponding phases elsewhere, the soils of this transect are characterized by a high proportion of coarse sand and a clay content which is rather high.

In the illuvial soils the proportion of total sand is large compared with that found in the other transects, figures for corresponding sites being as follows: Aweil 51 %, cf. Wau 21 %; Aweil 47 %, cf. Halima 33 %. This feature, together with the general abundance of coarse sand, may derive from a component of originally transported material. The latter is strongly suggested by the presence throughout the lower sites of pea-iron which has obviously been transported, and is rendered likely by the low relief of the region.

As to the considerable clay fraction in sites at all levels, it should be noted that the overall difference in elevation between the top and bottom of this long transect is very slight—probably less than 3 m. (10 ft.). It may well be, therefore, that even the higher sites receive water-borne material in years of exceptionally high flood. Such an occurrence is, of course, least likely in section I, whose relative abundance of clay has already been considered (p. 39) in comparison with similar soils from near Wau. From section II to section IX there is a progressive increase in clay content, reflecting the gradual drop in level. Section X seems at first glance somewhat anomalous in that its clay content does not continue this progression. Unlike the other illuvial sections, however, it belongs to the freely drained type (Il/Dr), of which it is the lower phase. (The upper phase, Il/Dr 1, represented by Transect I, section IV, was practically absent from the Aweil transect, although it was observed elsewhere in the neighbourhood, bearing extensive *Terminalia* communities.)

pH *values*

These show the same general trend as in the other transects. Acidity increases with depth in the E complex, decreases with depth in the Il complex, and is irregular in relation to depth in the Col complex. Section III is thought to be an old cultivation zone, in which the probable levelling of alkaline termite mounds might well account for the relatively high pH, approaching neutrality below 10 cm. (4 in.) depth.

Clay analysis

The silica content of the eluvial soil of section I is higher than that of the corresponding soils in the other two transects (54 % as against 45–47 %). This conforms to expectation in view of the lower rainfall of the Aweil district. Except on the eluvial complex, however, a high degree of clay decomposition is to be expected, since all the other soils consist of transported and re-sorted material. For the colluvial soil (section II) this is indicated by a silica percentage as low as 37, a remarkable drop which is reflected in lower SiO_2/R_2O_3 and SiO_2/Al_2O_3 ratios. The higher ratios in the various components of the illuvial complex are to some extent due to resilication and in section IX to a concurrent loss of alumina.

Table 12. *Transect III (Aweil); soil analysis*

	Section I			Section II				Section III		Section IV		Section VI		Section VIII	Section IX		Section X		
Soil phase	E/Dp		E/S.R	Col/F1				Col-II		Col-II		II/Id1		II/Id3†	II/Id2		II/Dr2		
Vegetation type	Ironstone woodland		Treeless area	Combretum				Entada transition		Combretum-Anogeissus transition		Upper Anogeissus		'Bauhinia'	Mitragyna		Grassland		
Cm. from surface	0–27	27–32	0–12.5	0–12.5	12.5–32	32–50	50–	0–10	10–	0–12.5	12.5–32	0–10	10–30	0–15	0–10	10–	0–10	10–30	30–60
Mechanical analysis (%):																			
Coarse sand	57.4	51.4	54.5	51.4	41.3	35.2	31.2	36.8	26.2	51.5	44.8	48.9	27.8	17.6	27.9	26.1	32.2	32.7	23.6
Fine sand	17.5	22.3	18.0	31.2	23.2	13.1	10.4	31.6	30.1	24.0	15.4	14.2	14.7	23.7	25.2	15.5	29.7	18.1	23.9
Silt	2.9	3.8	3.5	7.4	4.7	4.6	7.6	11.9	12.7	4.2	5.8	11.8	8.4	12.2	12.6	8.5	11.4	9.1	5.1
Clay	22.3	22.4	24.0	10.0	30.8	47.0	50.8	19.7	31.0	20.3	33.9	25.0	49.0	46.4	34.4	49.9	26.7	40.1	47.3
pH	6.0	4.7	5.3	5.9	4.7	4.6	5.0	5.6	6.7	5.0	4.4	5.5	5.1	6.0	5.2	5.9	5.5	5.8	6.0
Clay analysis:																			
SiO_2 (%)	53.9	.	.	37.2	.	.	.	.	.	52.6	.	53.2	.	51.0	53.5	.	(Values for this section from sampling of Aweil toich on an earlier expedition)	.	.
Al_2O_3 (%)	37.0	.	.	39.6	.	.	.	.	.	41.6	.	40.0	.	39.8	29.8	.		.	.
Fe_2O_3 (%)	9.0	.	.	6.4	.	.	.	.	.	5.8	.	6.4	.	7.3	10.3	.		.	.
SiO_2/R_2O_3 (mol. ratio)	2.14	.	.	1.45	.	.	.	.	.	1.97	.	2.05	.	1.94	2.63	.		1.9	1.9
SiO_2/Al_2O_3 (mol. ratio)	2.47	.	.	1.60	.	.	.	.	.	2.14	.	2.25	.	2.17	3.04	.		2.0	2.1
SiO_2/Fe_2O_3 (mol. ratio)	15.99	.	.	15.55	.	.	.	.	.	24.23	.	22.15	.	18.46	13.79	.		22.4	23.6
Al_2O_3/Fe_2O_3 (mol. ratio)	6.47	.	.	9.75	.	.	.	.	.	11.30	.	9.83	.	8.50	4.53	.		11.0	11.3

† In this section, designated by the frequent occurrence of *Bauhinia*, several soil phases were represented (text, pp. 70–1); sample taken from an II/Id3 site under *Acacia seyal*.

The SiO_2/Fe_2O_3 ratio in the eluvial soil (section I) is high (16) as compared with the figures for corresponding sites in the other transects (12 in both), reflecting the difference already noticed in silica content. The adjacent colluvial soil has the same ratio of 16, a similarity perhaps connected with the very small difference in level between the E and Col sites on this transect.

In the flooded sections from IV downwards, the two highest sections sampled, IV (Col-Il) and VI (Il/Id 1), show silica/ferric oxide ratios of 24 and 22; sections VIII (Il/Id 3) and IX (Il/Id 2), classed with VI as impeded illuvials, but more extreme, show distinctly lower values (18 and 14), apparently owing to removal of less iron. Section X is practically the same in SiO_2/Fe_2O_3 (22) as the upper sections IV and VI; although topographically the lowest section, its drainage is of a free type (Il/Dr 2) rather than impeded. In this group of ratios we may perhaps see an example of how the type of drainage, as well as mere topographical level, is involved in the development of these flooded soils.

VEGETATION RECORDS, TRANSECT III

A casual glance at Table 13 reveals two very evident features. There is an abundance of symbols, explained by footnotes, which refer to details of occurrence in relation to termite mounds or micro-relief. Secondly, the floristic 'drift' down the sections, though recognizable, is much obscured by a large proportion of species which occur very generally or without apparent relation to the sequence of sections. Both of these features are genuine reflexions of the nature of the Aweil catena-variant, whose differences in level are so slight that undulations on the small scale of micro-relief can cause much obscurity in a pattern which in a very broad sense is zoned. Although by no means an elegant demonstration of phase communities in sequence, this transect is nevertheless instructive; with a knowledge of the simpler form, as seen in Transect I, it shows how a highly confused system of mosaics, obscure zones and intergradations can occur without constituting any exception to the strict correlation of topography, soil and vegetation. Most of the apparent irregularities in the floristic drift in Table 13 can be explained in terms of micro-relief or termite mounds. Since the factual basis for this statement cannot be made directly apparent from the table, relevant points about floristic occurrence in relation to micro-relief and termite mounds are put on record as follows.

(i) A few of the species characteristic in sections I and II occur on level or slightly raised sites in sections III, IV and V; in section VI they show some preference for the more elevated termite mounds, and in sections VIII and IX this preference is very definite (e.g. *Stereospermum*). The diffuse distribution of occurrences down the section I column is thus explained by the undulating micro-relief throughout the transect, and in particular by the presence of termite mounds and other local elevations in the partially flooded lower sections.

(ii) Sections II–V contain species elsewhere seen to be characteristic of phases other than Col/F 1 and Col-Il, the two phases which these sections mainly represent. Of these 'intrusive' species, some are characteristic of eluvial sites (e.g. *Sclerocarya, Hexalobus, Crossopteryx*), others of illuvial sites (e.g. *Bauhinia, Combretum binderanum*). Such occurrences seem capable of explanation in terms of the very slight differences of level between these sections, combined with variations of micro-relief which in places cut across the

line of the transect; thus sites frequently occur which in topographical character (not necessarily in *level* as such) do not 'belong' to the sections in which they are included.

(iii) A major cause of interruption in the drift of flora as tabulated is the fact that most of the termite-mound species of sections VIII and IX are prevalent on mounds throughout the transect.

(iv) In addition to the species common to termite mounds at all or nearly all levels, a few are found only on mounds situated at the higher levels (e.g. *Hippocratea, Opilia, Capparis corymbosa, Adenia*), and a few only on lower-level mounds (e.g. *Bridelia scleroneuroides, Stereospermum, Combretum binderanum, Cassia, Antidesma, Andira*). The possible significance of differentiation between mound habitats has been discussed earlier (p. 13).

(v) In sections I, II and III, all the species not recorded as occurring on termite mounds were on flat ground. In section I, however, much of this ground was more or less affected by termite activity. In section III no mounds were present; they may have existed in the past.

(vi) In sections IV, V and VI, the sites of occurrence of many species are indicated by *(termite mounds) or ‡(intermediate between elevations and depressions). All other occurrences, except of the grass *Hyparrhenia* which was characteristic in depressions, were on obvious elevations most of which were probably of termite origin.

(vii) In section VII, which lacks termite mounds, all the woody species except *Acacia seyal* grow on low elevations. The latter, although not obviously of termite origin, appeared to fulfil the role of termite mounds as centres of growth because, like the mounds, they are less flooded than their surroundings. It may be noticed that most of the species localized in this way in section VII occur on termite mounds in neighbouring sections. Several of them appear to be at their optimum on the elevations in section VII.

Finally, four examples may be given to illustrate the kind of apparent divergence from typical behaviour which is indicated for certain species by the sign (¶) in Table 13. *Acacia hebecladoides*, found in sections II and III, was characteristically seen elsewhere in the neighbourhood in *Anogeissus* woodland like that of sections VI and VII. *Sarcocephalus esculentus*, found in sections II and IV, would be expected instead to occur frequently in section IX. *Ctenium elegans* was probably co-dominant, before burning, on the large areas of annual grass in section I, where it was recorded, after burning, as rare. *Lannea schimperi* is a characteristic ironstone species, and its record in section VIII represents its only observed occurrence on a termite mound.

V. SUMMARY

During an expedition to the south-western part of the Anglo-Egyptian Sudan in the dry season of 1938–9, data were collected with a view to elucidating the confused soil and vegetation types characteristic of African savanna-woodland country.

Despite the seemingly chaotic mixture in which the subordinate types occur, it was found that they could be distinguished, their mutual relationships recognized, and apparent correlations established with factors operating. This was made possible through the adoption of the following general thesis and its close application to the minor as well as major soil-vegetation units seen in the field. This thesis puts in a precise form the relation between rainfall, topography and the soil-vegetation complex—a relation well

known to exist and most easily seen in the tropics, but seldom worked out in terms of detailed, localized phenomena of soil and vegetation.

Basically the thesis maintains (subject to certain exceptions) that the development of the soil on any site is mainly determined by the local topography through its effect on water movement. Soils are thus divided primarily into three complexes: High-level (eluvial), slope (colluvial) and low-level (illuvial). Broadly speaking, eluvial soils lose material; colluvials gain and lose concurrently; illuvials gain material and are flooded. The resultant differences are, naturally, of major importance. Such a division involves the concept of a catena, or topographically determined sequence of soils, following the usage of Milne (1935). Recognition of this catenary arrangement, complicated by the mosaic form imposed by micro-relief, is combined with the observation that over extensive regions the recurring units of a particular soil type repeatedly bear plant communities with the same distinctive characteristics, and with the same or related floristic composition. This constant relationship is shown even by the most closely defined soil-type units (phases) and their vegetation, often on very small areas of ground.

The concept of the catena hence embraces soils and vegetation together. Thus is enabled the formulation of a comprehensive classification of minor and major soil-vegetation units and their relatively easy recognition in the field. Superimposed are the modifying effects of different steepness and length of slopes and of different rainfall, producing catena-variants with their own peculiarities of soil detail, floristic content and sometimes dominant species.

Such a method of approach to synecological problems, wherever local differences in the water conditions are not obviously subordinate in influence to some other factor or factors, seems capable of wider application than it has received. It can be used with advantage in the allocation of land for agriculture and forestry, notably in the seasonally dry tropics.

The south-western Sudan (map, p. 9) consists of a dissected peneplain with a gentle dip from south-west to north-east. The soils have a uniform geological origin, being derived *in situ* or by water carriage from basement gneiss; blown sand is, however, sometimes present in the northernmost part of the province visited. The vegetation over most of the area is savanna woodland, dominated by deciduous trees.

The area as a whole is divided into five natural regions distinguished primarily by topography and rainfall: (1) the jebel country in the immediate neighbourhood of rocky hills; (2) the watershed region on the south-western border, with narrow valleys and perennial streams; (3) the main tributary-river region with comparatively wide, shallow valleys in rolling country; (4) the almost level flood-plain region; (5) the permanent swamp or Sudd region.

The account which follows deals only with regions (3) and (4), which are considered jointly; region (3) is predominantly one of eluvial and colluvial soils and region (4) is very largely illuvial.

Emphasis is laid on the control of soil and vegetation by the alternation of marked dry and wet seasons, causing desiccation and local flooding, and on the profound effects of almost ubiquitous yearly grass fires, cultivation, erosion and termite activity. The main features of the soil-vegetation catena and complexes, as shown in regions (3) and (4) at large, are described on the basis of widespread observations and four sets of detailed records. The 'composite catena' thus derived is figured in a profile drawing (Fig. 2, p. 13).

The characteristics of each of the three soil-vegetation complexes, their phases and phase communities, as they were observed in the main tributary-river and flood-plain regions, are described in the sequence shown by the following table. The phases are designated by symbols which express the subdivisions of E (eluvial), Col (colluvial), and Il (illuvial). The eluvial phases are classified mainly on the basis of depth, the colluvials on texture, the illuvials on drainage conditions.

It should be understood that a grass layer (whose specific composition is often indeterminable in the dry season) is practically ubiquitous, forming the major part of the vegetation cover on sites where scattered trees are quoted as the vegetation 'dominants'.

Complexes and phases of the composite catena

Name of phase	Symbol	Vegetation dominants
Eluvial complex		
Eluvial deep	E/Dp	Trees, deciduous and evergreen
Termite mound on E/Dp site	E/Dp+	Trees, evergreen and deciduous
Eluvial shallow	E/S	Trees, deciduous
Eluvial shallow redistributed	E/S.R	Annual grass
Eluvial shallow eroded	E/S.Er	Small trees and shrubs (*Hymenocardia*)
Eluvial (ironstone) outcrop	E/O	No vegetation except in cracks and pockets
Eluvial-colluvial transition	E-Col	Trees, evergreen and deciduous (e.g. *Isoberlinia*)
Colluvial complex		
Colluvial coarse	Col/C	Trees (*Butyrospermum*)
Colluvial fine 1	Col/F 1	Trees (*Combretum*)
Colluvial fine 2 †	Col/F 2	Bamboo (*Oxytenanthera*)
Colluvial-illuvial transition	Col-Il	Trees, various
Illuvial complex		
Illuvial drained 1 (upper) §	Il/Dr 1	Trees, scattered (*Terminalia*)
Illuvial drained 2 (lower) §	Il/Dr 2	Perennial grasses (*Hyparrhenia*)
Illuvial impeded 1 (upper) ‖	Il/Id 1	Trees (*Anogeissus*)
Illuvial impeded 2 (lower) ‖	Il/Id 2	Trees, scattered (*Mitragyna*)
Illuvial impeded 3	Il/Id 3	Trees (*Acacia seyal*)
Illuvial undrained (basin site)	Il/U	Grass, with or without *Acacia seyal*

† Uncommon type depending on special conditions.

§ Rarely bearing termite mounds (Il/Dr 1+, Il/Dr 2+).

‖ Frequently bearing termite mounds (Il/Id 1+, Il/Id 2+).

The eluvial complex, whose phases occur mainly in the form of a mosaic, comprises the hard 'ironstone' of the higher ground and the soils and vegetation associated with it. This complex has the shallowest and coarsest soils. The deepest of them (apart from termite mounds) is the eluvial deep phase (E/Dp); this is apparently stable under present conditions and is dominated by a mixture of deciduous trees, with or without a small proportion of hard-leaved evergreens, over an understorey of smaller deciduous trees and shrubs and a herb layer dominated by tall perennial grasses. The specially favourable habitats produced by the superposition of termite mounds (E/Dp+) on this phase give rise to islands of vegetation including a higher proportion of evergreen trees, which shelter a dense thicket of smaller evergreen and deciduous trees, lianes, shrubs and herbs, grasses being almost eliminated. Parts of the mosaic where the A soil-horizon is less deep (E/S) bear a lower, more open, and entirely deciduous tree canopy, with deciduous shrubs, herbs and a dense layer of tall perennial grass. Mixing and redistribution of shallower variants of E/S seem the cause of the phase called E/S.R, whose vegetation is reduced mainly to annual grasses. The shallow, eroded phase (E/S.Er), in which the B 1 pea-iron horizon is exposed, bears a rather open thicket of shrubs, with annual and perennial grasses. The final result of erosion is an outcrop of the B 2 ironstone horizon; this phase (E/O) bears no vegetation at all except in cracks and pockets.

With sufficient slope and rapidity of erosion there is an accumulation of ironstone detritus between the edge of the eluvial complex and the upper colluvial zone; this E-Col transition zone is a particularly favourable habitat for certain evergreen and broad-leaved deciduous trees. The soils and vegetation of the eluvial complex are summarized in Table 1 (p. 17).

The colluvial soils, deeper and finer than the eluvials, are produced by the sorting of material mainly derived from the erosion of the eluvial mosaic. They form a zoned complex, or sub-catena, grading from coarse-grained shallow soils at the top of the slope (Col/C) to fine-grained deep ones at the bottom (Col/F), although the differentiation of separate colluvial zones varies according to conditions of slope and rainfall. By far the most common and characteristic colluvial zone is the fine-grained, red soil (Col/F 1) bearing a vegetation dominated by species of *Combretum*. This zone is a favourite site of cultivation; it is also subject to fierce fires. The latter circumstance alone may be sufficient to account for the absence of well-grown mixed woodland which, there is reason to suppose, could otherwise occur. Under existing conditions the colluvial complex is poor in characteristic species.

A transition zone (Col-Il) usually occurs between Col/F 1 and the illuvial complex, and may be very extensive where the slope is scarcely perceptible. This transition zone, situated at about the limit of normal flooding, is also widely cultivated and, with its groves of *Borassus* and other less gregarious, but conspicuous, preserved or planted trees, constitutes a main feature of the country, especially in and around the flood-plain region. The soils and vegetation of the colluvial sub-catena are summarized in Table 2 (p. 22).

The illuvial complex comprises those soils which occupy the seasonally flooded low-level ground. They are the deepest and generally much the heaviest soils. They are composed of colluvial material washed from adjacent higher ground by the rain-flood, with the addition (except in some minor valleys and small basin sites) of alluvial material carried from a distance by a general valley or plain flood. Micro-relief determines whether the illuvial phases are zoned or form a mosaic; its undulations induce the latter arrangement most obviously where the general slope is very gentle. Also correlated with micro-relief is the nature of the drainage. By this latter property two main groups of phases are distinguished, those with free and those with impeded drainage. This difference does not necessarily involve the occupation of a regularly higher level in the catena by one group than by the other. The illuvial drained phases (Il/Dr) occur where there is nothing to prevent flood-water draining away to an effective drainage-channel; the surface is even, though usually sloping very gently. Such terrain results in zonation rather than mosaics. The distinctive upper phase of this group (Il/Dr 1) bears an association characterized by spaced *Terminalia* trees; the lower phase (Il/Dr 2) bears the open *Hyparrhenia* grassland of the 'toiches', which are often extensive and provide such a familiar feature of the broader valleys and flood plains. The illuvial impeded phases (Il/Id) show signs of drainage-impedance. They are associated with uneven ground, which promotes mosaics of phases. From Il/Id 1 to Il/Id 3 there are, progressively, a greater degree of impedance, finer texture, and darker colour, culminating in the black soil of the completely undrained 'basin' site (Il/U). The tree vegetation of these impeded phases shows single-species dominance, which is especially characteristic of illuvial sites; in Il/Id 2, however, the trees (*Mitragyna*) are often far apart, with intervening grassland of 'toich' character though composed largely of *Vetiveria nigritana* instead of *Hyparrhenia*. The occurrence of termite

mounds, providing habitats raised above flood level and suitable for tree growth, is a characteristic feature of the two less markedly impeded phases. The soils and vegetation of the illuvial complex are summarized in Table 3 (p. 27).

As already explained, the generalized picture given by the foregoing account of the composite catena varies with conditions of topography and rainfall. Where these conditions are intermediate between the extremes encountered, as they are east of Wau, not only are all three complexes of the catena clearly represented, but also there is the clearest development of the E complex—the higher ground being broad enough for its micro-relief to vary repeatedly (cf. Halima variant, below) but not so flat as to make such variation relatively insignificant (cf. Aweil variant). Here, too, there is a relative abundance of evergreen trees, which have a marked influence on subordinate vegetation; evergreens are much rarer on the eluvial complex where the rainfall is either higher or lower. The colluvial complex is best developed where a somewhat higher rainfall associated with narrower and steeper ridges (Halima variant) causes more downward movement of eroded material; provided the lower slopes are long enough and not too steep, the colluvial material is then sorted out into two, or rarely three, distinct colluvial zones. Below them the illuvial complex is poorly represented in this variant owing to the absence of wide valleys. The illuvial complex is most elaborate in the flood-plain region, where it predominates. Here, with very gentle slopes (e.g. north of Aweil), the duration and mode of drainage of the seasonal flood have their greatest influence, while the elevation of the higher ground is so slight that between it and the flooded levels there is often no typical colluvial slope.

The catena-variants so produced form a series which may be summarized as follows:

Halima variant (main tributary-river region, upper parts)	Steepest topography and highest rainfall	E contracted, mosaic blurred Col well developed Il much reduced
Wau variant (main tributary-river region, lower parts)	Intermediate topography and rainfall	E well developed Col) moderately Il) developed
Aweil variant (flood-plain region)	Flattest topography and lowest rainfall	E simplified Col much reduced Il well developed

These variants differ in their characteristic plant species, which are listed in Table 4 (p. 35).

The account given of the catena, its complexes, phases and variants, is based on observations made in many places, but detail was added by the study of three transects representing the three catena-variants distinguished. The pedological, vegetational and floristic records from these transects are given in the last part of the paper. They are included in order to provide practical illustration of the fundamental soil-vegetation units, whose recognition is essential if the catena/mosaic interpretation of the soils and plant communities is to be successfully applied.

Transect I (Wau) shows a comparatively simple and distinct zonation which presents a clear picture of the catena sequence; it did, in fact, provide the key to the whole soil-vegetation problem. Associated with this first transect was a detailed study of the eluvial mosaic, especially of termite mounds. It was confirmed that the soil of the mounds contains a high proportion of clay, which seems to be washed out, especially near the surface, as the mounds become disused and collapse. This process is apparently accompanied by a change from an alkaline to a slightly acid reaction comparable with that in

the soil of the surrounding level ground. Many of the characteristic plants, which become established on the favourable site provided by the mounds, evidently fail to persist for long after the mound is obliterated. The mounds nevertheless play an important role in the development of the eluvial woodland as a whole, in general through interaction with the fire-factor and in particular because they encourage the establishment of *Khaya senegalensis*. This important evergreen canopy-tree persists as the characteristic dominant of the dense patches of vegetation on comparatively level sites probably occupied formerly by mounds.

Transect II (Halima), because of its interrupted slope, is composed of two catenas, its sequence of complexes being E →Col →E →Col →Il. The upper catena shows local dominance by *Isoberlinia*, one of the chief contributors to the vegetational appearance of the Halima catena-variant. The lower catena displays a particularly clear example of colluvial zonation, combined with the poor representation of illuvial ground which is a further characteristic of this variant.

Transect III (Aweil) shows a lack of clarity in zonation, due to a combination of very slight general slope with undulating micro-relief. A comparatively simple eluvial mosaic and a very extensive and rather confused but interesting illuvial complex are separated by ill-defined colluvial and colluvial-illuvial transition zones. In addition to irregularities of terrain, termite mounds make a very important contribution to the complexity of the whole transect.

Single samples of the various soils on these transects give analysis results corresponding well with those obtained by Greene (1939 and unpublished MS.) from similar soils in the Sudan. The following general points are derived from the figures. (i) Finer texture in lower horizons. (ii) Progressively finer texture from eluvial to colluvial and thence to illuvial soil. (iii) Coarser eluvial soils where steeper slopes and higher rainfall promote greater eluviation. (iv) All the soils (except those from termite mounds) are more or less acid. (v) With greater depth the acidity increases in eluvial and decreases in illuvial soils, while colluvials vary in this respect. (vi) Exchangeable calcium, determined for one transect, was most plentiful near the surface in soils from all three complexes. (vii) The silica/sesquioxide ratios of comparable eluvial samples, one from each transect, show a gradation of magnitude inverse to that of rainfall. (viii) In general this ratio is highest in illuvial soils, which are subject to resilication, and lowest in colluvials, whose material can on this account be considered more thoroughly weathered than that of the eluvials. (ix) The silica/ferric oxide ratio, controlled as it is by weathering, resilication and loss of ferrous iron, does not show a regular progression according to topographical level, but it seems likely to prove useful in characterizing the pedogenic conditions of the various phases.

Two features of a general kind may be noted in the tables recording the vegetation of the transects. (i) The 'drift' of species from the upper to the lower sections of each transect, the differences between the sections being most obvious in Transect I and least so in Transect III. (ii) The eluvial complex has by far the richest flora, although in Transect III the fact is obscured by the quantity of characteristic termite-mound species at lower levels. From each of the vegetation tables for the more complicated transects (II and III) closer study brings out a number of detailed points, several of which are noted as typifying the catena-variant concerned.

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APPENDIX

LIST OF SPECIES CITED

Including synonyms in common use

* Indicates species which occur characteristically on termite mounds.

Acacia albida *Del.*; syn. *Faidherbia albida* (Del.) A. Chev.; (Mimosaceae): Phot. 6

A. campylacantha *Hochst.* ex *A. Rich.*; syn. *A. suma* Benth., and of Broun & Massey, not of Kurz: Phots. 3, 34

A. drepanolobium *Harms*

A. hebecladoides *Harms*

A. seyal *Del.*; syn. *A. stenocarpa* Hochst.; see note under next entry: Phots. 30, 31, 32

A. seyal *var.* multijuga *Schweinf.* ex *Bak. f.*; widely known in E. Africa under the name '*A. stenocarpa* Hochst.'; *A. stenocarpa* Oliv. in part, and of Broun & Massey in part, not of Hochst.; probably more than varietally distinct from *A. seyal*

A. sieberiana *DC.*; confused by some authors with *A. verugera* Schweinf. and *A. rehmanniana* Schinz: Phot. 27

*Adenia venenata *Forsk.* (Passifloraceae)

Afrormosia laxiflora (*Benth.*) *Harms* (Papilionaceae)

Afzelia africana *Smith*; syn. *Pahudia africana* Prain; (Caesalpiniaceae): Phot. 14

Albizzia sericocephala *Benth.*; syn. *A. amara* Oliv., and of African authors, including Broun & Massey, not of Boiv.; (Mimosaceae)

A. zygia (*DC.*) *Macbr.*; syn. *A. brownei* Walp.: Phot. 3

Amblygonocarpus schweinfurthii *Harms* (Mimosaceae)

Ammocharis tinneana (*Kotschy & Peyr.*) *Milne-Redh. & Schweick.*; syn. *Crinum tinneanum* Kotschy & Peyr.; (Amaryllidaceae)

*Andira inermis (*Wright*) *Kunth* ex *DC.* (Papilionaceae)

Andropogon gayanus *Kunth* (Gramineae)

Annona senegalensis *Pers.* (Annonaceae)

*Anogeissus schimperi *Hochst. ex Hutch. & Dalz.*; the '*A. leiocarpus* G. & P.' of Broun & Massey; (Combretaceae): Phots. 3, 13, 29, 30, 31

*Anthericum sp. (Liliaceae)

Antidesma venosum *E. Mey.* ex *Tul.* (Euphorbiaceae)

Asparagus sp. indet. (Liliaceae)

Asteracantha longifolia (*L.*) *Nees*; the '*Hygrophila spinosa* T. And.' of Broun & Massey; (Acanthaceae)

*Balanites aegyptiaca *Del.* (Simaroubaceae): Phot. 29

Barleria grandicalyx *Lindau* (Acanthaceae)

Bauhinia thonningii *Schum.*; the '*B. reticulata*' of Broun & Massey, not of DC.; (Caesalpiniaceae): Phots. 31, 34

Beckeropsis uniseta (*Nees*) *Stapf* ex *Robyns*; the '*Pennisetum unisetum* Benth.' of Broun & Massey; (Gramineae)

Borassus aethiopum *Mart.*; syn. *B. flabellifer* L. var. *aethiopum* Warb.; (Palmaceae)

*Boscia salicifolia *Oliv.* (Capparidaceae)

*B. senegalensis (*Pers.*) *Lam.* ex *Poir.*; syn. *B. octandra* Hochst. ex Radlk.

Bridelia micrantha (*Hochst.*) *Baill.* (Euphorbiaceae)

B. scleroneuroides *Pax*

Bulbostylis coleotricha (*Hochst.*) *C.B.Cl.* (Cyperaceae)

Burkea africana *Hook.* (Caesalpiniaceae): Phot. 16

Butyrospermum parkii *var.* niloticum (*Kotschy*) *Pierre* (Sapotaceae): Phots. 9, 20, 21, 28

*Cadaba farinosa *Forsk.* (Capparidaceae)

Canthium malacocarpum (*K. Schum. & K. Krause*) *Bullock* (Rubiaceae)

*Capparis corymbosa *Lam.* (Capparidaceae)

*C. persicifolia *A. Rich.* var.

*C. rothii *Oliv.*

Carissa edulis *Vahl* (Rubiaceae)

*Cassia singueana *Del.*; syn. *C. goratensis* Fres.; (Caesalpiniaceae)

Chlorophora excelsa (*Welw.*) *Benth. & Hook. f.* (Moraceae)

Cissus cornifolia (*Bak.*) *Planch.* (Ampelidaceae)

*C. quadrangularis *L.*

Cochlospermum tinctorium *Perr.* ex *A. Rich.* in *G. & P.*; syn. *C. niloticum* Oliv.; (Cochlospermaceae)

Combretum (Combretaceae): Phots. 1, 9, 18, 20, 21, 22, 26

*C. aculeatum *Vent.*

C. binderanum *Kotschy*; '*C. collinum*' in Broun & Massey, in part, the Mongalla plant: Phot. 29

C. ghasalense *Engl. & Diels*

C. glutinosum *Perr.*

C. lecananthum *Engl. & Diels*; syn. *C. brunneum* Engl. & Diels

C. undulatum *Engl. & Diels*; the '*C. undulatum* Wall.' of Broun & Massey, at least in part

C. verticillatum *Engl.*

Cordyla richardii *Planch.* ex *Milne-Redh.*; the '*C. africana*' of Broun & Massey, not of Lour.; (Caesalpiniaceae)

Courbonia virgata *A. Brongn.* (Capparidaceae)

Crateva adansonii *DC.*

Crossopteryx febrifuga *Afz.* ex *G. Don*; syn. *C. kotschyana* Fenzl; (Rubiaceae)

Ctenium elegans *Kunth* (Gramineae)

Cymbopogon giganteus (*Hochst.*) *Chiov.* (Gramineae)

Cyperus papyrus *L.* (Cyperaceae): Phots. 6, 7

Dalbergia melanoxylon *G. & P.* (Papilionaceae)

Daniellia oliveri (*Rolfe*) *Hutch. & Dalz.*; the '*D. thurifera*' of Broun & Massey, not of Benn.; (Caesalpiniaceae): Phot. 8

Detarium senegalense *J. F. Gmel.*; syn. *D. microcarpum* G. & P.; (Caesalpiniaceae)

*Diospyros mespiliformis *Hochst.* ex *A.DC.* (Ebenaceae): Phot. 36

Entada sudanica *Schweinf.* (Mimosaceae): Phots. 27, 28

Erythrophleum africanum (*Welw.*) *Harms* (Caesalpiniaceae)

Euphorbia bongensis *Kotschy & Peyr.* (Euphorbiaceae)

*E. candelabrum *Trém.* ex *Kotschy*

Ficus capensis *Thunb.* (Moraceae)
F. platyphylla *Del.*
F. vallis-choudae *Del.*: Phot. 3

Gardenia aqualla (*Schweinf.*) *Stapf & Hutch.* (Rubiaceae): Phot. 19
G. erubescens *Stapf & Hutch.*
G. lutea *Fres.*: Phot. 30
G. triacantha *DC.*
Gnidia kraussiana *Meisn.*; the '*Lasiosiphon kraussii* Meisn.' of Broun & Massey; (Thymelaeaceae)
Grewia mollis *Juss.* (Tiliaceae)
*G. villosa *Willd.*
Gymnosporia senegalensis (*Lam.*) *Loes.* (Celastraceae)

Hexalobus monopetalus (*A. Rich.*) *Engl. & Diels* (Annonaceae)
Hibiscus sabdariffa *L.* (Malvaceae)
*Hippocratea richardiana *Cambess*; the '*H. obtusifolia* Roxb.' of Broun & Massey; (Hippocrateaceae)
Hymenocardia acida *Tul.* (Euphorbiaceae): Phots. 8, 14, 19
Hyparrhenia (Gramineae): Phot. 11
H. barteri *var.* ¿calvescens (*Hack.*) *Stapf*
H. dissoluta (*Nees*) *C. E. Hubbard ex Hutch.*; the '*H. ruprechtii* Fourn.' of Broun & Massey
H. rufa (*Nees*) *Stapf*: Phots. 5, 10

Indigofera binderi *Kotschy* (Papilionaceae)
I. bongensis *Kotschy & Peyr.*
I. bracteolata *DC.*
I. hendecaphylla *Jacq.*
Irvingia smithii *Hook. f.* (Simaroubaceae)
Isoberlinia doka *Craib & Stapf* (Caesalpiniaceae): Phots. 14, 16, 17

Jussiaea suffruticosa *L.*; the '*Jussieua villosa* Lam.' of Broun & Massey; (Onagraceae)
Justicia betonicoides *C.B. Cl.* (Acanthaceae)

Khaya grandifoliola *C.DC.*; syn. *K. dawei* Stapf *ex* Broun & Massey; (Meliaceae): Phot. 2
*K. senegalensis *A. Juss.*: Phots. 12, 25, 26, 28
Kigelia aethiopica *Decne.* (Bignoniaceae)

Landolphia comorensis *var.* florida *Benth. K. Schum.*; syn. *L. florida* Benth. (Apocynaceae)
L. owariensis *var.* tomentella *Stapf*
*L. petersiana *var.* schweinfurthiana (*Hall. f.*) *Stapf*
*L. senegalensis *var.* glabriflora *Hua*
Lannea (Anacardiaceae)
L. kerstingii *Engl.*; as to leaves = *Lannea barteri* (Oliv.) Engl., the type of which is a mixture with flowers of *L. schimperi*; also = the '*Odina* cf. *O. Barteri*' of Broun & Massey, e descript.
L. schimperi (*Hochst.* ex *A. Rich.*) *Engl.*; syn. *L. barteri* (Oliv.) Engl. (*Odina barteri* Oliv.), as to flowers only. (Some of the material cited (by locality) in Broun & Massey under *Odina schimperi* and *O. barteri* is really *L. kerstingii*.)
*L. schweinfurthii (*Engl.*) *Engl.*: Phots. 29, 35
Lepidagathis appendiculata *Lindau*; under *L. radicalis* in Broun & Massey; (Acanthaceae)
L. sp. *aff.* fischeri *C.B.Cl.*
Lonchocarpus laxiflorus *G. & P.* (Papilionaceae)

*Maba abyssinica *Hiern* (Ebenaceae): Phot. 13
Maerua angolensis *DC.* (Capparidaceae)
*M. harmsiana *Gilg*
Manilkara schweinfurthii (*Engl.*) *Dubard*; syn. *Mimusops schweinfurthii* Engl.; (Sapotaceae)
Mitragyna inermis (*Willd.*) *O. Kuntze*; syn. *M. africana* (Willd.) Korth.; (Rubiaceae): Phots. 24, 34, 35, 36
*Mystroxylon aethiopicum (*Thunb.*) *Loes.*; syn. *Elaeodendron aethiopicum* (Thunb.) Oliv.; (Celastraceae)

Ochna sp. (Ochnaceae)
Oncoba spinosa *Forsk.* (Flacourtiaceae)

*Opilia celtidifolia (*G. & P.*) *Endl.* ex *Walp.*—The '*O. amentacea*' of Broun & Massey is a misidentification— (Opiliaceae)

Oxytenanthera abyssinica (*A. Rich.*) *Munro* (Gramineae): Phot. 23

Parinari curatellifolia *Planch.* ex *Benth.* (Rosaceae)

Parkia oliveri *Macbr.*; syn. *P. intermedia* Oliv., non Hassk.; the '*P. filicoidea*' of the Flora of West Tropical Africa and of Broun & Massey, not of Welw.; (Mimosaceae): Phot. 27

Pavetta schweinfurthii *Bremek.* (Rubiaceae)

Pennisetum pedicellatum *Trin.* (Gramineae)

*Popowia djurensis *Engl. & Diels* (Annonaceae)

Prosopis africana (*G. & P.*) *Taub.*; syn. *P. oblonga* Benth.; (Mimosaceae)

Protea madiensis *Oliv.* (Proteaceae)

Pseudocedrela kotschyi (*Schweinf.*) *Harms* (Meliaceae): Phot. 31

Pterocarpus abyssinicus *Hochst.*; the '*P. lucens*' of Broun & Massey, probably not of G. & P.; (Papilionaceae): Phot. 9

Randia nilotica *Stapf* (Rubiaceae)

*Rhus natalensis *Bernh.* ex *Krauss*; syn. *R. glaucescens* A. Rich.; (Anacardiaceae)

Rhynchosia caribaea (*Jacq.*) *DC.* (Papilionaceae)

*Sansevieria sp. HS 182 & 219 (Liliaceae)

Sarcocephalus esculentus *Afz.*; syn. *S. russegeri* Kotschy; (Rubiaceae): Phots. 5, 27

Sclerocarya birrea (*A. Rich.*) *Hochst.* (Anacardiaceae): Phot. 25

Sporobolus sp. probably *S. festivus* Hochst. ex A. Rich. (Gramineae)

Sterculia setigera *Del.*; syn. *S. tomentosa* G. & P. non Thunb.; (Sterculiaceae): Phot. 29

Stereospermum kunthianum *Cham.* (Bignoniaceae): Phot. 27

Striga barteri *Engl.* (Scrophulariaceae)

Strychnos innocua *Del.* (Loganiaceae): Phot. 8

S. spinosa *Lam.*

*Tamarindus indica *L.* (Caesalpiniaceae): Phot. 13

*Teclea nobilis *Del.* (Rutaceae)

Terminalia (Combretaceae): Phots. 1, 11

T. glaucescens *Planch.* ex *Benth.* (?); syn. *T. schimperiana* Hochst. & *T. salicifolia* Schweinf.

T. laxiflora *Engl. & Diels*: Phot. 10

T. macroptera *G. & P.*; syn. *T. dawei* Rolfe: Phot. 11

T. mollis *Laws.* sensu lato; the '*T. torulosa*' of Broun & Massey, probably not of F. Hoffm.

Urginea indica (*Roxb.*) *Kunth* (Liliaceae)

Vetiveria nigritana (*Benth.*) *Stapf* (Gramineae): Phot. 34

Vitex doniana *Sweet*; syn. *V. cuneata* Thonn. & *V. cienkowskii* Kotschy & Peyr.; (Verbenaceae): Phot. 3

V. madiensis *Oliv.*

Wissadula amplissima var. rostrata (*Schum.*) *R. E. Fries*; syn. *W. rostrata* (Schum.) Hook. f.; (Malvaceae)

*Ximenia americana *L.* (Olacaceae)

Xysmalobium heudelotianum *Decne.* (Asclepiadaceae)

*Ziziphus abyssinica *Hochst.* ex *A. Rich.* (Rhamnaceae)

*Z. mauritiana *Lam.*; syn. *Z. jujuba* Lam. non Mill. & *Z. orthacantha* DC.

AN INDEX FOR ESTABLISHING THE DEGREE OF MATURITY IN PLANT COMMUNITIES

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The purpose of this paper is to introduce an index which may be used as a datum of orientation in statistical studies of plant communities.

In carrying out the investigations in a community we usually make the floristic list of the species present in a certain number of sample plots scattered over the ground under examination. This work, carried out on the spot, enables us to establish what species are present therein and calculate with sufficient accuracy what is the frequency percentage with which the single species appear.

With these data we are in a position to construct a table in which are listed the names of the species present in the community with their respective frequency percentages and to calculate the biological spectrum of the community on the basis of the different life forms to which the separate species belong. The table and the biological spectrum accompanied by other data collected on the site itself, e.g. vitality, stratification, etc., allow us to give a sufficiently accurate description of the quantitative and qualitative characteristics of the community in question.

However, in order to give a clearer picture of the vegetation, in addition to these data I thought it useful to introduce a new datum, which I have named 'maturity index'.

The maturity index is the quotient of the total of the frequency percentages of all the species in the community—a total which Raunkiaer* calls 'points'—divided by the number of the species found on the station. This reflects the long-accepted notion that the higher the frequency percentage of each species and the smaller the number of sporadic species, the more mature the plant community.

The calculation of the maturity index is very easy, since the points, as well as the number of the species, are not only easily calculable, but also indispensable for obtaining the biological spectrum of the community in question. As an example of calculation of the maturity index I take the following communities (Table 1) studied by Raunkiaer and quoted on p. 339 of the collected papers of the author.†

Calculating the maturity index for these communities and integrating the data already calculated by Raunkiaer, we obtain the spectrum given in Table 2.

The maturity index, to the best of my knowledge, is now introduced for the first time into the statistical studies of vegetation. It affords us a datum of orientation for establishing the maturity of plant communities, which may be of some use in the study of the development of the vegetation.

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* Raunkiaer introduced the term 'points' in 1909–10 ('Investigations and statistics of plant formations' in *The Life Forms of Plants and Statistical Plant Geography being the Collected Papers of C. Raunkiaer*, VI, pp. 201–82, Oxford, 1934). In this publication he, however, calculated the points on a basis of fifty sample plots. It was only in 1913 ('Statistical investigations of plant formations of Skagens Odde' in Raunkiaer, loc. cit. VIII, pp. 303–42) that he adopted 'points' on a basis of 100 sample areas, as all other authors still do to-day.

† Raunkiaer, loc. cit., 1934.

In calculating the maturity of plant communities, great importance has been attributed to the frequency with which every species appears in the community, and especially to the number of those which are dominants, i.e. those which appear with a frequency superior to 80%.* Importance has also been given to the percentage proportion these plants show with respect to all the other species taken together. This criterion is certainly right, but in my opinion it is not sufficient to enable us to ascertain the degree of development reached by the vegetation. A community lacking in dominants and in which some frequent species appear, accompanied by a large number of sporadic species, has a different value from a community in which a few dominants appear accompanied by a smaller number of frequent species and sometimes by still fewer sporadic plants.

Table 1. *Localities in the moss dune of Skagens Odde* (25 × 0·1 sq.m.)

	Life form	1	2	3	4
Koeleria glauca	H	100	92	72	96
Weingaertneria canescens	H	92	52	—	60
Carex arenaria	G	88	100	100	92
Sedum acre	Ch	8	—	—	—
Thymus serpyllum	Ch	4	—	—	84
Veronica officinalis	Ch	—	8	64	56
Agrostis vulgaris	H	—	—	40	—
Anthyllis vulneraria	H	—	—	4	4
Artemisia campestris	H–Ch	—	8	—	—
Campanula rotundifolia	H	8	—	60	24
Festuca rubra	H	64	100	100	96
Galium verum	H	16	4	4	72
Hieracium umbellatum	H	—	4	—	—
Hypochoeris radicata	H	—	4	—	—
Jasione montana	H	8	60	40	12
Lotus corniculatus	H	24	24	4	20
Armeria vulgaris	H	4	—	—	20
Viola canina	H	—	—	—	16
Linaria vulgaris	G	—	—	36	—
Poa pratensis	G	—	8	28	—
Psamma arenaria	G	4	40	24	40
Cerastium semidecandrum	Th	—	—	—	12
Teesdalea nudicaulis	Th	—	16	4	—
Viola tricolor	Th	—	32	4	—
Points		420	552	584	704
No. of species		12	15	15	15

Table 2

	Points	No. of species	Maturity index	Ch	H	G	Th
No. 1	420	12	35	3	75	22	—
No. 2	552	15	37	1	63	27	9
No. 3	584	15	39	11	56	32	1
No. 4	704	15	47	20	59	19	2

In the first case we are dealing with a community in which some species have succeeded and achieved some importance but not so much as to dominate and to eliminate the numerous other species, which appear sporadically and are less adapted to the ecological conditions of the station. A community of this kind has evidently failed to exploit all the possibilities of life which the environment offers to plants, and is therefore heterogeneous, incoherent and liable to more or less important changes. On the contrary, in the second case, the community is made up of a few species all well established, which

* Determined by 0·1 sq.m. plots ('The area of dominance, species density, and formation dominants' in Raunkiaer, loc. cit. xvi, pp. 517–46).

occupy all the free space, reducing the sporadic species to a minimum or excluding them outright. Communities of the second type present a population more homogeneous, close and less liable to infiltration by new species, and thus more solid in its composition.

Of these two kinds of communities, the second is, in my opinion, maturer than the first, not only because the separate species forming it are better distributed, but also because they take advantage of all the possibilities of life offered by the environment. Every plant has managed, more or less successfully, to establish itself, adapting itself to the conditions of the station and achieving a certain balance with the other members of the community. This balance is, of course, temporary, but its temporary nature is more lasting than that of the community of the first type in which a certain number of sporadic species lead us to suppose that the plant population of the station is settling down.

In plant communities the separate species compete with one another, each trying to expand as much as possible and gradually preventing the less adapted species from settling on the station. This ruthless competition ends by eliminating from the community the species less adapted, and at the same time by increasing the frequency of those which are more adapted.

In order to calculate the degree of maturity of a community it is therefore necessary to consider two values above all others: the number of the species present in it, and the frequency percentage of each separate species. For this reason I thought it best to introduce into the statistical study of plant communities the maturity index, based, as I have already mentioned, on these two values.

As the frequency of separate species is expressed in percentage value, it is obvious that the value of the maturity index must vary between 0 and 100, and naturally the more highly developed the community, the nearer to 100 its maturity index.*

Before I introduced the maturity index into the study of vegetation, it was tested both in several previously known investigations and also in others which were carried out myself specially for this purpose. In all cases I remarked that whenever the value of the maturity index is low, the vegetation shows evident marks of immaturity, while every time it is high, the vegetation is, on the contrary, advanced. Of these many instances two examples only need be quoted: the first relates to the study of the vegetation of an area, the second to the study of a plant population of a particular habitat.

In the study of vegetation of the ophiolitic soils of the Upper Tiber Valley,† I have applied the maturity index to the statistical investigations of the plant communities. In this work we can see straight away how the maturity index increases along with the evolution of the vegetation. In fact, if we examine those communities of the serpentine soil, which are not far advanced, as, for instance, those of the screes or of the calanchiform stations, we can see that the maturity index attains a value under 15. If we take, instead, the pasture communities which now represent the climax of this soil in the Upper Tiber Valley, we see that the maturity index reaches the highest value (about 40). In opposition to pastures, woods do not represent in these serpentine soils an advanced kind of vegetation. They are never of spontaneous growth, but always intruders from neighbouring soils

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* The maturity index may be calculated by any method in which the frequency is measured, even in the cases in which a scale of five classes, from 1 to 5, is used. In this case it is obvious that the value of the maturity index will be included between 1 and 5.

† **Pichi-Sermolli, R. (1948).** 'Flora e Vegetazione delle serpentine e delle altre ofioliti dell' Alta Valle del Tevere (Toscana).' *Webbia*, **6**, 1–378, Firenze. (In the Press.)

of different edaphic nature. In proof of this I may recall that woods are present only in those localities in which the serpentine soil is in contact with other soils; that trees penetrate into serpentine soils accidentally, both in the case of more pedologically advanced stations and in that of less advanced ones; that woods only manage to expand with extreme slowness; finally, that the species of these wood communities belong to different kinds of vegetation. The value of the maturity index of these wood communities is low, and varies from 11 to 20. In this case too, as in others, the maturity index supports the conclusions which have been reached through the study of the other characteristics of plant communities.

If, in another example, we compare the maturity index of each of the four communities studied by Raunkiaer and quoted above, we see that the maturity indices of communities nos. 1, 2, 3, 4, are respectively 35, 37, 39, 47. If we bear in mind the species dominating in each community, we note that with the increase in the maturity index there is also an increase in the value of chamaephytes. This leads us to suppose that vegetation on the dunes of Skagens Odde, originally formed of hemicryptophytes and geophytes, is changing, along with the microclimatic conditions and the consolidation of that soil, into a type of vegetation where the chamaephytes are acquiring an important place beside the other two life-forms.

The maturity index, as a ratio between the points and the number of species present in a community, expresses the average of the percentages of frequency of all the species, and thus gives the average percentage frequency. In practice, the maturity index is equivalent to the percentage frequency of a species which in the composition of the community has an average importance between the frequency of dominants and that of sporadic species. Thus the introduction of the maturity index leads to the introduction of the concept of 'average species'—a purely theoretical concept which, together with that of dominants, clearly expresses the degree of maturity reached by the vegetation. In fact, this concept takes into account the fact that dominants are accompanied by frequent and sporadic species, which, as I have already pointed out, are very important factors in the estimation of the maturity of communities, particularly of those not far advanced.

We cannot, however, attribute to the maturity index an absolute value, but only a relative and directive one, as we must take into account the type of vegetation of the community. We cannot, for example, when studying the vegetation of a particular area, arrange the various communities one after another according to the maturity index, mixing up communities of screes, pastures, meadows, steppes, woods, peat lands, fens, etc. If we did this, we should put together different kinds of vegetation without taking into consideration the environmental conditions in which they live and the real affinities existing between them; but above all we should fail to take into consideration the climax which these types may attain. We may, nevertheless, arrange all the kinds of communities which form part of a single line of evolution in accordance with the maturity index. In this way, the index allows us to set up these kinds in an ascending series which really reflects the way of evolution which vegetation follows in order to reach the climax toward which it is tending.

Those types of communities which do not follow the normal way of evolution, but which develop as a particular kind dependent on special local conditions, are, of course, to be considered separately. In their case too, however, the maturity index is helpful for us, not only in arranging the various communities, but also in realizing their degree of

maturity by means of a comparison with the indices of the communities forming part of the vegetation we regard as normal in the area under observation. Actually, by taking the average of the various indices of one kind of community and comparing it with those of other kinds, we are in a position to judge the degree of maturity of that kind compared with others, and thus to put it in its right place in the vegetation of the area taken as a whole.

From what we have said above, it is evident that the maturity index allows us also to realize to what climax the vegetation of a particular area or a given kind of station, characterized by special ecological conditions, is progressing. Actually, in both cases the communities which have the highest maturity index are those nearest to the climax to which the vegetation of that area or that particular station is tending.

The maturity index supplies us also with a datum of comparison, however approximate, enabling us to determine the degree of maturity reached by a single type of vegetation in two different areas. A comparison between the various maturity indices of the same kind of lowland heath, or wet heath, or pedunculate oak wood, or sessile oak wood, or beech wood, etc. of different areas would, I am sure, give us useful information as to the degree of evolution of these different types of vegetation. It would also allow us to establish in what area each type under consideration reaches its highest maturity, i.e. in what area we can find the most genuine expression of the type of vegetation in question.

The maturity index is also useful in the study of altitudinal belts of vegetation, enabling us to determine at what altitude we find the most advanced and genuine communities of the types of vegetation representing the various zones and horizons. Studying, for instance, the altitudinal zonation of the vegetation at the various altitudinal levels of a particular region of the Apennines, and carrying out investigations in the communities in the various zones and horizons and at the tension belts, and comparing the investigations of these communities, we are able by means of the maturity index to establish at which level we find the most genuine expression of pubescent oak wood, chestnut wood. beech wood, etc.

Before concluding this article I wish to repeat once more that I do not mean to give the maturity index an absolute value, but only a relative and directional one. I recognize that to give the indices for the statistical studies of vegetation a strictly mathematical value, as some authors do, is tantamount to accepting a false picture of the vegetation of a community. Indeed no investigation, however accurate it may be, and no index, even the clearest, can ever give us an exact picture of the plant population of a station, which, as it results from the combined action of multiple and multiform environmental local factors, is to the highest degree discontinuous and unstable.

SOMMARIO

Scopo di questa nota è l' introduzione nello studio statistico della vegetazione di un nuovo indice (indice di maturità), che può servire come dato di orientamento per valutare la maturità dei consorzi vegetali.

L' indice di maturità è il quoziente tra il totale delle percentuali di frequenza delle singole specie del consorzio ed il numero delle specie presenti nella stazione.

Questo indice rispecchia la nozione già da tempo acquisita, che un consorzio vegetale è tanto più maturo quanto più alta è la percentuale di frequenza delle singole specie e più piccolo il numero delle essenze sporadiche.

Siccome la frequenza delle singole specie è espressa in valori percentuali, l'indice di maturità è compreso tra 0 e 100 e naturalmente un consorzio è tanto più maturo quanto più il valore del suo indice di maturità si avvicina a 100.

L'introduzione dell'indice di maturità, quale media tra le percentuali di frequenza delle singole specie, porta all'introduzione del concetto di 'specie media', concetto puramente teorico che insieme a quello di specie dominante esprime chiaramente il grado di maturità raggiunto dalla vegetazione.

L'indice di maturità ha solo un valore relativo e nell'applicarlo deve essere tenuto conto del tipo di vegetazione del consorzio, evitando di confondere insieme consorzi che non appartengono alla stessa linea evolutiva della vegetazione. Tenendo presente questo, è possibile sistemare tutti i tipi di consorzi in base all'indice di maturità in una serie ascendente la quale realmente rispecchia il cammino evolutivo che la vegetazione percorre per raggiungere il climax verso il quale essa tende.

L'indice di maturità oltre che allo studio della vegetazione di una determinata regione, è utile nel confronto tra consorzi dello stesso tipo viventi in territori diversi, permettendoci in questo caso di stabilire in quale di essi ciascun tipo di vegetazione raggiunge la sua massima maturità. Anche nello studio dei limiti altimetrici della vegetazione l'indice di maturità ci offre un utile dato; infatti esso ci permette di stabilire a quale altitudine noi riscontriamo l'espressione più genuina dei consorzi caratteristici dei vari piani ed orizzonti altimetrici.

THE EFFECT OF ARCTIC AND HIGH MOUNTAIN CLIMATES ON THE CARBOHYDRATE CONTENT OF *OXYRIA DIGYNA*

BY R. SCOTT RUSSELL, *Department of Agriculture, University of Oxford**

During the Imperial College Expedition of 1938 to Jan Mayen in the Greenland Sea, some physiological and ecological studies of plant growth under arctic conditions were undertaken (Russell & Wellington, 1940; Russell *et al.* 1940; Russell, 1940). The results of these preliminary studies seemed sufficiently promising to justify further field investigations of plant growth in cold climates. Two features of the arctic climate are clearly outstanding, namely, low temperature and continuous daylight, and it was felt that a useful approach for distinguishing between the effects of these two factors would be a comparative study of plant growth in the Arctic and among high mountains in temperate regions. These two habitats have the common characteristics of a short growing season and a low mean temperature, but the diurnal patterns of the two climates contrast sharply. In the Arctic, during summer, light of low intensity is continuous throughout the 24 hr. period, while in temperate regions the duration of daylight is limited, but its intensity at noon is particularly great at high altitudes. Since day length is dependent on latitude the contrast between such environments will clearly be greatest if the high mountain habitat is in a low latitude with a short day length.

In 1939 the British Karakoram Expedition, led by Mr Eric Shipton, gave the writer an opportunity for studying a particularly suitable high mountain vegetation. Eighteen months were to be spent in the Karakoram-Himalaya, which lie at the latitude of 35° N. between Kashmir and Chinese Turkistan. The vegetation at the altitude of 12,000–15,000 ft. is in many ways similar to that of Jan Mayen at sea-level. *Oxyria digyna* occurs in both localities.

The outbreak of the European war in 1939 caused work to be abandoned at an early stage. Of the fragmentary physiological results which were obtained, one series, however, merits attention as it enables a comparison to be made of the carbohydrate content of *O. digyna* in the two localities.

Unfortunately, a general ecological description of the vegetation of the Karakoram cannot as yet be prepared as the Herbarium collections await detailed examination; a brief preliminary description is, however, available (Shipton, 1940). For present purposes it is sufficient to note that the general facies of the community in which *O. digyna* grows in the Karakoram is similar to that in Jan Mayen (Russell & Wellington, 1940).

THE JAN MAYEN RESULTS

Before considering the Karakoram data it is desirable to review the results from Jan Mayen in relation to carbohydrate metabolism. High levels of total carbohydrates (starch and total sugars) are found at the beginning and the end of the growing season, sometimes amounting to 40% of the alcohol-insoluble material. At midsummer the general level of carbohydrate in the plant is considerably lower. A close connexion between temperature

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and the partition of carbohydrate between starch and soluble sugars has been found; low temperature favours the hydrolysis of starch.

It appears that assimilation is retarded by low temperature to a lesser degree than are the growth processes in which it was utilized. The resultant high levels of carbohydrates have considerable ecological significance. Rapid development in early spring is a characteristic of many arctic plants. It enables them to make the maximum growth and to develop to maturity in the short growing season. Development may commence (as was found with *O. digyna* on Jan Mayen) when the plants are still covered with several feet of snow. Particularly in its early stages, this rapid development is dependent on the large reserves of carbohydrate stored in the root stock and not on new assimilatory products. The declining carbohydrate content of the root stock in early summer provides evidence of this. Annual species would appear on these grounds to be little suited to arctic climates, unless the seed contains a large proportion of stored food relative to the total growth of the plant. It is of interest that only one annual species (*Koenigia islandica*) was found on Jan Mayen Island. Its distribution was restricted to particularly favourable environments.

High levels of soluble carbohydrates are usually characteristic of frost-resistant plants in temperate regions (Anderson, 1944; Levett, 1941). Whether this accumulation of carbohydrate is to be regarded as the primary factor determining cold resistance is debatable, but it is generally held to be at least an important contributory factor. This suggests that a high carbohydrate level in arctic plants may not only be important for ensuring rapid spring growth but also for protecting the perennating root stock from frost damage during winter.

These considerations led to the conclusion that a capacity for accumulating carbohydrates in high concentration is an important characteristic of plants growing in an arctic environment.

KARAKORAM RESULTS

Two series of replicated samples of mature leaves of *Oxyria digyna* were made at approximately 4 hr. intervals for 24 hr. at Makorum beside the Hispar Glacier at the altitude of 12,500 ft. Sampling and analytical methods were similar to those employed in Jan Mayen (Russell, 1940).

Series I was taken on 2–3 August when the period of active growth was ending and anthesis had lately occurred; and Series II on 26–27 September when fruits were mature but the leaves had not yet died back. Both series were collected on sunny days and the air temperatures, recorded by the dry bulb of a whirling hygrometer, may be taken as representative of the prevailing conditions (see Table 1). The first sample was taken at approximately the warmest time of the year. No continuous temperature observations are available.

COMPARISON OF JAN MAYEN AND KARAKORAM RESULTS

The results of the two Karakoram series are summarized in Table 2, together with Jan Mayen data for plants of comparable growth status to Series II.

Between the three samples there is a remarkably close agreement in the total carbohydrate content and in the ratio of reducing sugar to total sugar. Starch values by contrast are highly variable. The decline in the starch level between the first and second

Karakoram samples can be attributed to falling temperature. Unfortunately, no sample of leaves was taken on Jan Mayen at a stage of growth comparable to Karakoram Series I, but on Jan Mayen entire plants were sampled at various times and the results indicated that the maximum starch value occurred at the time when the leaf sample was taken. Thus on Jan Mayen it appears that starch values never approached to the high level found in the Karakoram Series I; neither in Jan Mayen did the temperature ever approach the maximum recorded when the first Karakoram series was taken.

Table 1. *Diurnal variations in light intensity, temperature and humidity on 2 days at Makorum, Karakoram-Himalaya, alt. 12,500 ft.*

Time (hrs.)	Light intensity (f.c.)	Air temperature (° C.)	Relative humidity
Series I. 2–3 August 1939			
21.00	Nil	5·8	41
01.00	Nil	4·7	93
05.00	18	− 1·7	100
09.00	1300	5·6	41
13.00	2700	19·4	13
17.00	72	16·1	5
21.00	Nil	5·6	46
Series II. 26–27 September 1939			
18.00	30	5·0	20
22.00	Nil	− 1·1	96
02.30	Nil	− 9·4	100
07.00	192	− 8·0	100
11.00	1920	11·7	21
14.00	960	8·9	22
18.00	70	5·6	23

Table 2. *Summary of results of observations on the carbohydrate content of leaves of* Oxyria digyna *in the Karakoram-Himalaya and Jan Mayen Island*

State of plants	Karakoram, Series I Anthesis	Karakoram, Series II Fruits mature	Jan Mayen Fruits mature
Temperature (° C.):			
Mean	8·9	1·3	7·6
Max.	22·0	12·5	10·2
Min.	− 2·5	− 11·0	6·4
Light intensity (f.c.):			
Max.	2700	1920	1375
Min.	Nil	Nil	2·5
Hours of daylight per day	14·75	13	24
Relative humidity:			
Max.	100	100	100
Min.	5	20	80
Mean carbohydrate content expressed as a percentage of the alcohol-insoluble material:			
Starch	11·03	2·20	3·47
Reducing sugar	6·43	12·97	11·88
Total sugar	9·98	19·31	18·37
Total carbohydrate	21·01	21·51	21·84
Ratio: reducing sugar to total sugar	0·64	0·67	0·64

Considering now the diurnal variations (Table 3), it is seen that the lowest total sugar value occurred in both Karakoram series towards sunrise and the highest in late afternoon. A similar trend is shown by the other carbohydrate fractions except reducing sugars in Series I. The variations are in general similar to those observed on Jan Mayen (Russell,

1940, p. 296) despite the very different variation in light intensity. It should be emphasized, however, that observations of diurnal variation for single 24 hr. periods in the field are of limited significance since they must reflect climatic changes. The primary object of taking the samples was in fact to obtain a valid daily mean.

Table 3. *Diurnal variation in carbohydrate content of leaves of* Oxyria digyna *at Makorum, Karakoram-Himalaya*

Time (hr.)	No. of replicates	Starch	Reducing sugar	Total sugar	Total carbohydrate
		Series I. 2–3 August 1939			
21.00	2	12·87	6·29	11·27	24·14
01.00	2	—	6·70	9·27	—
05.00	3	6·55	6·07	9·13	15·68
09.00	3	11·16	7·20	10·01	21·17
13.00	3	11·65	6·21	11·10	22·75
17.00	3	14·40	6·96	10·50	24·90
21.00	3	9·59	5·82	7·81	17·44
Mean		11·03	6·43	9·98	21·01
		Series II. 26–27 September 1939			
18.00	1	3·26	15·63	25·05	28·31
22.00	1	1·87	13·01	20·15	22·02
02.30	2	1·76	14·63	19·53	21·29
07.00	3	1·81	10·23	14·73	16·54
11.00	3	1·80	9·76	16·34	18·14
14.00	3	2·99	11·42	17·87	20·86
18.00	3	1·96	16·10	21·53	23·49
Mean		2·20	12·97	19·31	21·51

Summary and conclusion

The comparison of the carbohydrate content of mature leaves of *Oxyria digyna* growing at the altitude of 12,500 ft. in the Karakoram-Himalaya and at sea-level on Jan Mayen in the Arctic shows a surprising similarity with regard to total carbohydrate content, the ratio of reducing sugar to total sugar and the range of the diurnal variation. The agreement between the total sugar levels in both localities is somewhat surprising and suggests that when the level of carbohydrate is high it may tend to reduce the assimilation rate.

While the data are too limited to justify detailed discussion they indicate that the balance between carbohydrate formation and utilization is similar in the two environments despite the very marked dissimilarity with respect to diurnal climatic variation. Observational evidence suggests that growth rates too are not greatly different. In particular it is of interest that exposure to continuous daylight of low intensity in the Arctic appears to have had no special effect. The effect of the temperature differences between the two environments appears to be confined to determining the form of carbohydrate and not its total quantity. It must be understood, however, that detailed comparative investigations under field conditions must be made before this conclusion can be fully sustained. Moreover, the desirability of parallel studies in lowland temperate habitats is obvious.

In conclusion, it is suggested that in the study of the physiology of environment field sampling techniques provide a method which justifies much wider application than it has hitherto received.

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STAGES IN INVASION AND REPLACEMENT DEMONSTRATED BY SPECIES OF *MELANDRIUM**

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(With five Figures in the Text)

CONTENTS

INTRODUCTION

The origin of this study was in an attempt to investigate the autecology of the two British species of *Melandrium* and to make an assessment of their true status. From this inquiry it became apparent that they had not arrived in the British Isles at the same time, and that their relations with each other were not static. For this reason, the various stages which might be found in the invasion of an area containing one species by another were worked out and the correspondence of populations of the campions with this scheme examined. Such an investigation has been called for by Huxley (1938) who says: 'If two differentiated but interfertile populations meet as a result of migration, and one (*A*) has a slight selective advantage over the other (*B*), then *A* might slowly increase its area, while the intergrading zone is pushed into *B*'s area without increasing appreciably in width. I believe that the theoretical analysis of such a situation could prove fruitful, while in certain cases observational evidence as to such a shift of the intergrading zone could be obtained.'

The following article is an attempt to provide both a theoretical analysis and evidence from nature of the occurrence of such interaction.

* The substance of this article is abstracted from a thesis accepted by the University of London for the degree of Ph.D. (Baker, 1945).

STAGES IN INVASION

At the beginning, a region may be pictured containing a single form which would be well adapted to the conditions prevailing in at least a portion of that region. Having existed there for a considerable period natural selection would probably have operated to cause the form to be better adapted to these conditions than to most others. The form would have increased its adaptation at the expense of its adaptability. Such a state of affairs prevails in this country, for example, with the genus *Digitalis* which is represented here by one species only, *D. purpurea* Linn., although others exist in Europe and North Asia. Other species may be more variable and show many ecotypes. The extent of ecotype development depends upon the variability of the environment within the region and the number of genotypes available within the species. This condition may be designated *Stage* 0.

When, by extension of its geographical (including altitudinal) range, another closely related form enters the region, either by natural means or as a result of human activities, several consequences are possible. If the forms were differentiated originally as a result of ecological isolation the possibility is that natural selection would have caused the erection of a sterility barrier between them. This barrier may be of any degree of completeness. If it renders the two forms completely inter-sterile, whatever happens no hybridization could occur. If the barrier is incomplete, but the resulting hybrids are sterile or nearly so, the result is much the same. If the original differentiation was a result of geographical isolation it is not necessarily the case that the forms would be inter-sterile and the hybrids resulting from a cross might have only very slightly impaired fertility. Whatever their origins, if the species are inter-fertile, there are several possibilities. It is very unlikely that the two forms would have identical ecological requirements and, therefore, they would tend to occupy different associations or different societies within the same association. The societies occupied by the two forms might be separated by a considerable distance and, as a consequence, there would be little or no hybridization. *Veronica spicata* Linn. (sensu stricto) and *V. hybrida* Linn. are kept apart by adaptation to continental and oceanic climates, respectively. The well-known case of *Silene maritima* With. and *S. cucubalus* Wibel provides another example, although here the spatial separation is not perfectly complete (vide Marsden-Jones & Turrill, 1928–40). Not only may spatial separation keep the forms from hybridization but different flowering times or adaptation to pollination by different insects may perform the same function. Such isolation mechanisms are seldom highly efficient, however, and would not have the same complete effect as spatial separation.

If the forms should come to occupy adjacent societies an opportunity for cross-pollination would be presented. Where the boundaries between the societies are drawn sharply, and selection is strong in each case, it is unlikely that many of the poorly adapted first-generation hybrids would grow to the fruiting stage, and the inter-fertility would be of no consequence except that a certain amount of the seed-output would be wasted. However, if there is a zone of gradation between the societies, or if one or both of the societies are capable of supporting the first-generation hybrids, then their growth could take place. This would be followed by back-crossing to the form characteristic of each society and, of the resulting combinations, those most nearly resembling the original inhabitants in characters of significance for the original ecological difference would probably prove

superior and tend to be selected. Thus, the eventual effect as far as these characters are concerned would be small, but the genes responsible for the expression of characters which are neutral as far as this distinction is concerned would tend to be distributed through both populations. This condition may be designated *Stage* 1.

Should the invasion follow a modification within the region such that the original habitats and populations occupying them are cut off as 'island relics', these populations are more likely to show characters derived from the other species than are populations of the invader, which would form a meshwork between. In the latter population alien characters would tend to be swamped, while, for the relict species, decrease in the abundance of pollen-parents makes hybridization more likely.

A further stage may be envisaged in which the forms would be found in the same society. This might take place in rare instances when the two forms have identical or nearly identical ecological requirements, but the more likely cause is the modification of one or both habitats. Such modification may be brought about by the plants themselves, or by other plants or animals including man. If both habitats are modified so that both forms persist only as relicts their demise would be likely unless the modified habitats are intermediate between the two extremes, when it is possible that some hybrid-combinations might be successful. With the modification of one habitat alone so that only the form inhabiting it originally persists as a relict, inability of the other form to obtain admittance would result in the eventual dying-out of the ill-adapted relict. However, if the other form is admitted or the modification, though insufficient to admit this second form, permits the growth of a greater variety of the hybrids, then characters excluded formerly would be expressed. This may be called *Stage* 2.

In such cases a state of equilibrium would be formed, eventually, the composition of which would depend upon the extent of the modification and the severity of the subsequent selection. If the conditions should be relatively little altered, the balance would be struck at a point where the resultant population resembles the original more nearly than if the modification had been severe. On the other hand, in the extreme case this process might cause the complete disappearance of the original form except for neutral characters. This last may be called *Stage* 3. It is *Stage* 2 and *Stage* 3 which include what Anderson & Hubricht (1938) have called 'introgressive hybridization'.

Such a sequence of events may occur throughout a time period in one locality but every part of a region will not be likely to be affected to the same degree at the same time, and this fact is of great value in tracing the history of the relations of such a pair of forms. If the introduction of the immigrant form occurs at one locality, and the form spreads from here there will be developed a cline of hybridization (which should not be confused with the *nothocline* of Melville (1939)). Such a cline will differ from that mentioned by Huxley (1942) in his consideration of Allan's data upon *Alseuosmia* in New Zealand. This was a *primary* cline in which the two forms were differentiating. That with which we are concerned is an *invasion*-cline for which the term *xenocline* (*xenos* (Greek), alien) is proposed. This is of a secondary nature and the two forms may exhibit, elsewhere, a primary cline such as Allan describes. A xenocline may exist in two forms corresponding to topoclines and ecoclines, respectively, the former showing as a gradation of average values for populations across a region and the latter as a gradation of values across a population which overlaps more than one society.

The two campions illustrate very clearly some of the stages of this scheme.

Melandrium dioicum and M. album

Relationships

Carl Linnaeus (1753) described *Lychnis dioica*, consisting of three forms α, β and γ. The first was a red-petalled form, the second white-petalled and the third intermediate in this respect. Subsequently, α and β were separated as distinct species by several authors. The third form (γ) has been recognized, fairly generally, as a hybrid between α and β. The synonyms for both α and β are very numerous, and *Melandrium dioicum* (L. emend.) Coss. and Germ. and *M. album* (Mill.) Garcke are the most recent determinations for the respective species (vide Baker, 1945, 1947a). The close relationship between the species, observed by Linnaeus in uniting them and by numerous authors since who have described natural hybrids, has been confirmed by others who have made hybrids by artificial crossing.

The species are not separated by any perfectly efficient barriers, although there is a slight difference in the pollination mechanisms. The flowers of *M. dioicum* are diurnal in their opening and are pollinated by bees and butterflies, while those of *M. album* are nocturnal and are pollinated by moths. Also, there is a certation effect favouring the pollen of the same species as the pistillate plant. To these differences must be added a slight difference in phenology. The hybrid possesses considerable fertility and shows hybrid vigour. Where the two species come into contact they may be expected to form hybrids which will, themselves, intercross and backcross to the parents forming a hybrid swarm. Löve (1944) has regarded the two forms as ecotypes of the same ecospecies, while Baker (1945) has given evidence for regarding them as ecospecies of the same coenospecies.

In the British Isles, *M. dioicum* is chiefly an inhabitant of deciduous woodland (although it may be found occupying sheltered niches between rocks above the tree-limit). It is especially vigorous in the lighter phases of the coppice-cycle and may form a characteristic society with *Galeobdolon luteum* Huds. and *Euphorbia amygdaloides* L. when the coppice is cut (Tansley, 1939). It demands a well aerated but damp soil with a plentiful supply of nitrates. On the other hand, *Melandrium album* is, most frequently, a weed of cultivated fields and waste ground, never being found far away from the scenes of human activity (for further details of both species, vide Baker, 1945, 1947a).

Ancestry

There can be little doubt that *M. dioicum* and *M. album* are derived from a common ancestral species. Avebury (1905) stated that the ancestor was probably red-petalled but gave no evidence. Bateson (1913) speculated that they might have arisen from *Lychnis macrocarpa* Boiss. et Reut. (= *Melandrium divaricatum* Fenzl.) but he had very few facts and, himself, suggested that the latter might be a 'segregated combination' after all. There is a considerable possibility that *M. album* is derived from a species very like the present-day *M. dioicum*. Although *M. album* is only very slightly gregarious it shows the same dioecious nature as the highly gregarious *M. dioicum* for which this is much more favourable. The former species shows isolated plants, even in the regions where it occupies natural habitats (e.g. Palestine and Sinaii (Post, 1932)). The prevailing petal colour in the genus *Melandrium* (and even in the wider *Lychnis*) is red. Many of these red-petalled species have white-petalled varieties derived from them. *Melandrium album* represents what Onslow (1925) has called a 'partial albino', a type which does not usually appear to give rise to coloured varieties.

It has been found that populations of *M. album* (which are unlikely to have suffered inter-specific hybridization) show much greater variation in leaf thickness, 'leaf-index', flower diameter, calyx-tooth length, capsule size and height of plant, for example, than those of the lowland ecotype of *M. dioicum*. This, too, may be an indication of more recent origin. Herbarium studies show that, on the average, the leaves of plants of *M. album* growing in woodland shade in Spain and southern France are rounder than those produced by the species in this country. However, it has not yet been possible to demonstrate any definite ecotypes for this species which, as a consequence, may be referred to the first stage in Du Rietz's scheme of the development of a species (Du Rietz, 1930). *M. dioicum* has fairly well-defined ecotypes and is certainly in the second stage (vide Baker, 1945, 1947 *a*).
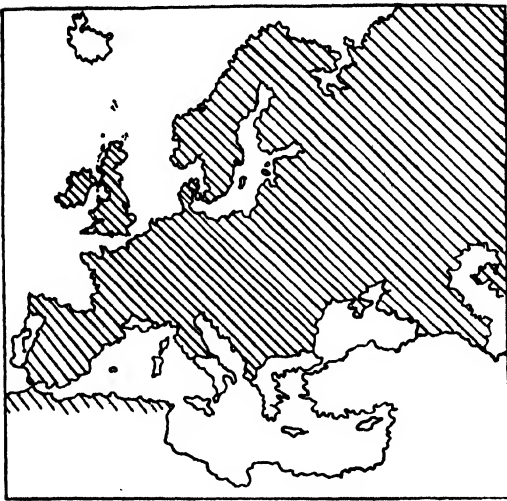
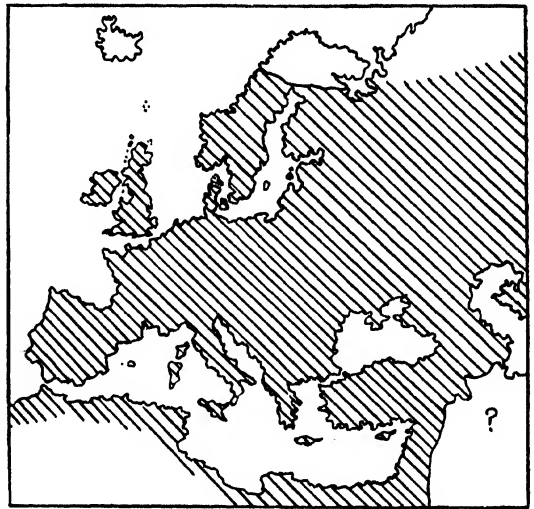Fig. 1. European and western Asiatic distribution of *Melandrium dioicum*.

Fig. 2. European and western Asiatic distribution of *Melandrium album*.

General history and distribution

Seeds of *M. dioicum* have been found in Interglacial remains in Britain and they occur again in the alpine Dryas-clays, which include not only the typical 'Dryas-flora' but other plants typical of woodland and marsh (Schroeter, 1926). The first Continental record of *M. album* is from the Swiss lake-dwellings (Hegi, 1931) which are of late Neolithic and Bronze Age (Wright, 1937).

The European and west Asiatic distributions of each species, as far as the literature and herbarium specimens reveal, are shown in Figs. 1 and 2. The close approximation of the areas is evident but there are significant differences. *M. album* has not penetrated as far into the arctic regions as has *M. dioicum* and it would appear that the northern agricultural limit is important in restricting the distribution of this species. Perhaps the most important differences are to be found in southern Europe and the Middle East. *M. dioicum* is absent and *M. album* is present at least in Gibraltar, the Mediterranean plain of France, southern ·Italy and Sicily, Sardinia, Corsica, Greece, Turkey, Armenia, Syria, Lebanon, Palestine, Sinaii and Libya. The latter species is more common, also, in Portugal, where

the existence of *M. dioicum* is doubtful (Continho, 1913), in parts of Spain, and in Algeria and Morocco.

Post (1932) described *M. album* as occurring in rocky places in Palestine and Sinaii, and Boissier (1867) reported the species from natural habitats in Macedonia, Armenia and Lebanon. Sibthorpe (1806) recorded the same for Byzantium (Istanbul), and de Halácsy (1900) did so for Thessaly. Specimens are in the herbaria at Cambridge University and the Royal Botanic Gardens, Kew, from natural habitats in Persia, and there is a probability that this species occurs in natural habitats in the southern and central Russian republics. Sterner (1922) includes this species in his list of plants introduced into south Sweden which have a native abode in the flood-meadows of central Russia (both species reach as far eastwards as the Altai Mountains and Lake Baikal). Throughout the Mediterranean region the species is found in meadows (Flahaut, 1937) and woodland, as well as less natural habitats; and even as far north as the north-western German Lowlands it is recorded from open woodland (Buchenau, 1894) and bushy hillsides (Dunn, 1905), although it is much more frequent as a cornfield weed. In the British Isles it is found only in or near man-made habitats. Dunn (1905) remarks upon its record in Normandy, Holland, Belgium and the British Isles as a weed supported by man. *M. dioicum* is found in natural habitats throughout Europe and reaches Spitzbergen and the east coast of Greenland, the possession of an arctic alpine ecotype making this possible. Its more northerly distribution is paralleled by a greater altitudinal range (Baker, 1945, 1947 a).

Huxley (1942, p. 155, etc.) has pointed out that sterility barriers are not *necessary* between forms which have diverged following geographical isolation. The lack of such a barrier between the species in question fits with the difference in geographical distribution mentioned above. It is likely that the origin of *M. album* was a result of ecogeographical divergence and that the Middle East was its home.

History and distribution in Great Britain and Ireland

Post-glacially, *M. dioicum* has been recorded from Boreal and Sub-Boreal remains, while *M. album* is recorded first from Neolithic (=Sub-Boreal, cf. Tansley, 1939, p. 150) beds àt Fife while subsequent records are from an early Bronze Age site at Fargo, near Stonehenge. The species may be represented among weeds of cultivation found in deposits at the site of the Roman city at Silchester, Hampshire (vide summary in Baker, 1945, 1947 a). The advent of the Neolithic Age corresponded with an increase of agriculture (probably first upon the chalk, oolitic and sandy soils) and further destruction of forest after that of the Mesolithic Age, in which latter period, Britain appears to have been populated by food-gatherers who had little influence on the vegetation (Tansley, 1939, p. 150).

Thus, the reported remains of *M. album* are of a later date than those of *M. dioicum* and show a correlation with the beginning of man's agricultural activities. In Historical time, deforestation and the spread of agriculture (which became especially marked in the twelfth century) have continued hand in hand, and the opportunities for *M. album* have increased at the expense of the habitats of *M. dioicum*.

The present geographical distributions of the two species in this country are given in detail in another publication (Baker, 1947 a) and need only brief recapitulation. *M. dioicum* is not definitely absent from any vice-county in Great Britain although it is very rare in Cambridgeshire and Huntingdonshire. Its abundance *increases* towards the north and

west. The distribution of this species, although described correctly by Watson (1847) as 'British', shows a leaning towards an 'Atlantic' character. The correlation of this with the relatively hygrophile nature of the species and its intolerance of severe winter conditions should be noted. Very different is the British distribution of *M. album*, which is commonest in East Anglia and the south-east of England and *decreases* towards the north and west. In Scotland, north and west England and Wales it is common only in regions which have been disturbed extensively by man. Its abundance in south-eastern and eastern England links it with the more extreme 'Germanic' type, with which it agrees in its preference for chalky and light soils and its tolerance of a rather 'Continental' climate.

There is every reason to believe that *M. album* is spreading at the present time, and some idea of its spread since the middle of the nineteenth century may be gauged from the works of Watson and his successors in the investigation of topographical botany. These show a gradual extension of the species into Scotland and the Isle of Man. Thus, there is some reason for believing that the present distribution of *M. album* is determined, in part, by the incompletion of its establishment in this country.

Fig. 3, which shows the *relative* frequencies of *M. dioicum* and *M. album* in the vice-counties of Great Britain and Ireland, brings out the difference. In Ireland neither species has the widespread distribution that it possesses in Great Britain. *M. dioicum* is rare in the centre (Praeger, 1934) and its only frequent occurrences are in some of the coastal counties. There does not appear to be any evidence that *M. dioicum* has not completed its spread, in fact, the opposite is likely to be the case. *M. dioicum* and *Geum rivale*, despite their rarity in the Dublin flora, occur in the relics of native woodland (*Euonymus europaeus* and *Viburnum opulus*) found in the glens on the western slopes of Mount Seskin Harbour (Colgan, 1904). The spread of *Melandrium album* does not appear to have been rapid in Ireland for a comparison of the lists given by Praeger (1901, 1934) shows only the addition of West Meath. It is localized in the south and east (cf. Britain). Most species which favour light soils are commoner in the east than the west (Praeger, 1901) but there is another possible correlation, for the arable land of Ireland is largely confined to the eastern counties. In most of the Irish floras *M. album* is referred to as a 'colonist' or with the reservation 'possibly introduced'. *M. dioicum* has reached the Shetlands and the Faeroe Islands, but records of *M. album* in the former are doubtful and lacking for the latter. Local variations in the occurrence of both species are found (Baker, 1945, 1947*a*) and appear to concern soil conditions and the amount and kind of agriculture.

CRITERIA OF HYBRIDITY

Ideal characters

Criteria for the reliable diagnosis of hybridity in natural populations have been drawn up elsewhere (Baker, 1947) and all suggested characters must be examined for their relations to these criteria.

Application to the campions

Gagnepain (1896, 1897), Compton (1920), Bentham & Hooker (1937 edition) and several authors of local floras have suggested possible means of distinguishing inter-specific hybrids in the campions, seldom using the same characters and not always preserving freedom from direct disagreement. Consequently, artificial crosses were made

between representatives of the two species (selected for their agreement with the type characters and taken from populations which were unlikely to be hybridized) and the resulting generations were grown in an experimental garden at Sunbury-on-Thames, Middlesex. The influence of the environment was tested by transplantation and field experiments. The detailed results of the genetical investigations will be published elsewhere, although they have appeared in Baker (1945), and a summary of the typical appearances of both species and the inheritance of the more useful characters is given in Baker (1947 a).
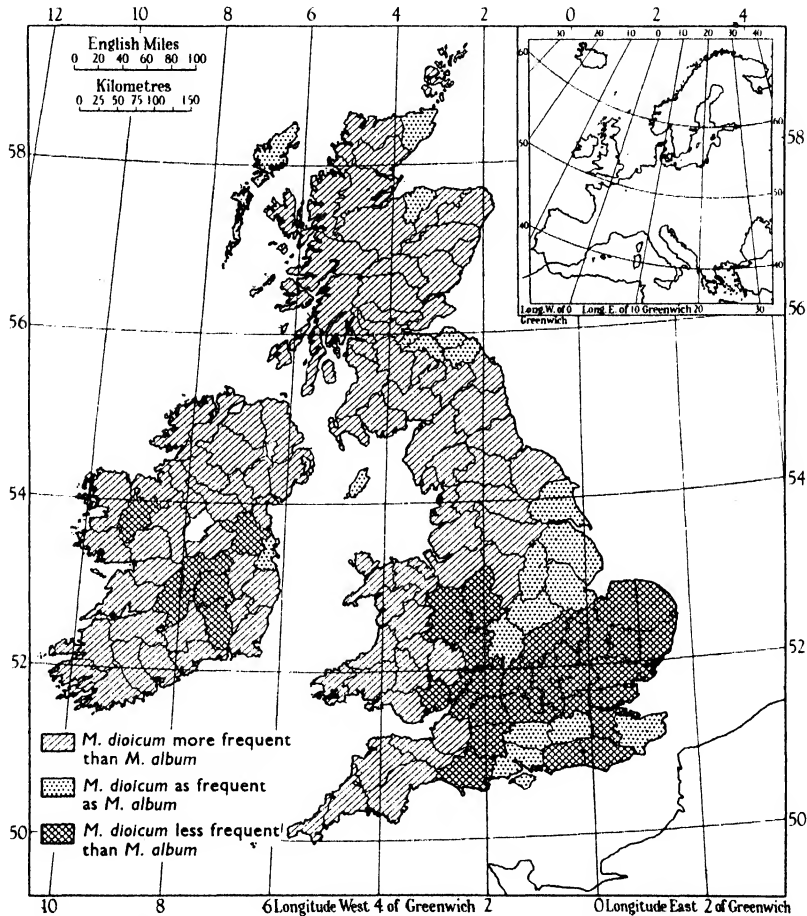

Fig. 3. Relative frequencies of *Melandrium dioicum* and *M. album* in the vice-counties of Great Britain and Ireland. For European distribution see Figs. 1 and 2.

The experimental investigation showed that the most conveniently investigated character for the diagnosis of hybridization in the history of a population is the length of the calyx-teeth. This is a 'constitutive' character, relatively uninfluenced by the environment although obviously depauperate flowers or those smutted by *Ustilago violacea* (Pers.) Fuckel (cf. Baker, 1947 b) must be avoided. Measurements upon pistillate and staminate flowers were averaged separately and a grand average for the population made from these (pure *M. dioicum* averaging from 2 to *c.* 2·8 mm. and *M. album* 4·5 to 6 mm.).

Investigations of populations of both species can, with advantage, include determinations of pollen sterility and the diameter of the pollen grains; direction of capsule teeth; capsule size and shape; pedicel length and position of leafy stolons. In certain cases the diameter and colour of the corolla (the latter especially in populations of *Melandrium album*); colour, weight and morphology of seeds; leaf-index (the ratio of the length of the lamina to its greatest breadth); thickness of leaves; presence of glandular hairs and form of root system are useful. The ability of the plants to flower in their first season is not determinable easily, neither is susceptibility to infection by a particular strain of *Ustilago violacea*, but these characters have their uses. Various characters concerned in the outward aspect of the plants may help in directing attention to the investigation of those characters which are more reliable and conveniently and accurately determinable.

A diagnosis of the exact status of each individual plant in the populations studied was not necessary and, consequently, no attempt was made to use an index method of the kind advocated by Anderson (1936). An average value for the population was worked out, usually, and recorded together with a note of the range between the extreme values. The selected characters were used in making field observations in three separate regions of Great Britain and samples of the detailed results are given below.

FIELD OBSERVATIONS
Wales

Observations in this region may be described first because they show, to a greater degree than any others, what must have been the primitive condition in these islands. *Melandrium dioicum* is common in every vice-county of Wales but *M. album* is far less common except in the east of South Wales. In the arable districts of Monmouthshire, Glamorgan and Brecknockshire the latter species is found as a weed and hybridization has occurred here. In the Gower peninsula of Glamorgan the introduction of *M. album* has taken place rarely and recently. Samples of *M. dioicum*, kindly sent to the author by Miss Irene Williams, B.Sc., from stations in this peninsula showed the populations to be free from hybridization, a determination which was confirmed, subsequently, by personal observation. A very interesting series taken from a site between Gowerton and Penclawdd showed the effect of the appearance of a plant of *M. album* (probably from seed introduced with nearby ballast) upon the population of *M. dioicum* inhabiting the area.

Populations observed at Pontsticill and Grawen, Brecknockshire, showed purity. Further specimens were received from Cenarth and Llechryd in Cardiganshire, both dairy farming areas. These showed no evidence of hybridization. These results are supported by the examination of preserved specimens in the herbaria, especially that of the National Museum of Wales, Cardiff. The conclusion may be drawn that, except in the eastern border counties, the invasion of Wales by *M. album* has not proceeded very far and that most of the populations of *M. dioicum* are still in the primitive (*Stage* 0) condition.

South-eastern England

Only two of the areas in south-eastern England which were investigated very carefully are described (for fuller details, vide Baker, 1945).

(i) *Sunbury, Walton and Weybridge area (Fig. 4)*

This area in south-western Middlesex and north-western Surrey is divided by the River Thames and this division coincides with a boundary between relatively heavy and

light soils, respectively. Within historic times this area was afforested but the natural woodland has disappeared completely. On the Middlesex side, *M. dioicum* is found in one relic population only, in the wild garden of Halliford Manor, which, by the kind permission
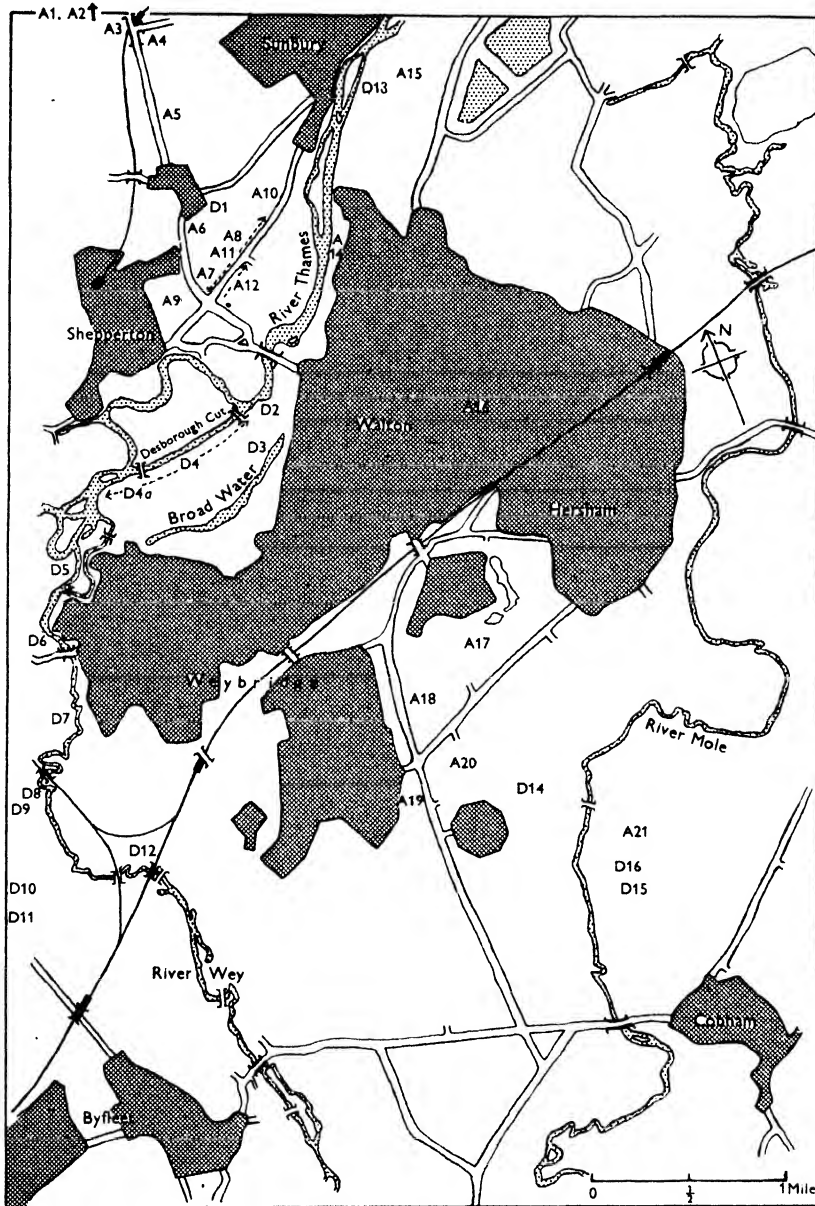

Fig. 4. Map showing the locations of populations of the campions investigated in the Sunbury, Walton and Weybridge area of Middlesex and Surrey. Largely built-up areas are cross-hatched.

of Mr C. R. B. Williamson, the author was enabled to investigate. Table 1 shows that this population (D1) had suffered some hybridization in its history and the occurrence of extensive populations of *M. album* in the fields around showed the cause. This 'island'

Table 1

Population	Description of habitat	Calyx-tooth length in mm. (grand average of ♂ and ♀)	Leaf-index (range of extremes in parentheses)	Range shown by direction of capsule teeth*	Range of petal colour†	Average % pollen sterility (range of extremes in parentheses)	Sex ratio (♀/♂)	Average thickness of ground-leaves in μ (determined in winter)
A 1–2	Waste land	4·4	3·71 (2·90)	—	—	—	—	—
A 3–5	Grass banks	4·6	3·92 (2·59)	Er	W	19·6 (37–4)	1·13	----
D 1	Elm Wood	2·9	1·76 (1·01)	Ro	W–R	13·8 (25–6)	—	256
A 6	Grass bank	4·4	4·06 (1·57)	Er	W	—	4·00	—
A 7	Hedgebank	4·7	4·33 (1·94)	Er	W	21·3 (50–2)	—	—
A 8	Cultivated field							
A 9	Cultivated field	4·7	4·09 (2·53)	Er	W	10·3 (39–0)	—	—
A 10	Waste mound	4·5	—	Er–Re	W–P	—	—	—
A 11	Hedgebank	4·7	4·21 (4·46)	Er	W	19·2 (59–0)	1·20	—
A 12	Hedgebank	4·5	3·05 (2·22)	Er–Re	W–P	—	—	—
A 13	Waste bank	5·5	3·20 (1·81)	Er	W	5·3 (13–2)	0·89	—
D 2	Ash and oak relic (grass invaded)	2·6	1·98 (1·64)	Ro	R	11·8 (39–0)	1·01	252
D 3	Oak wood with coppice	2·4	1·53 (0·68)	Ro	P–R	10·2 (27–0)	1·00	239
D 4	Towpath bank	3·5	2·56 (2·13)	Re–Ro	P–R	22·8 (71–0)	1·08	288
D 4a	Towpath bank (white-petalled plants)	5·0	4·07 (1·15)	Er	W	—	—	—
D 5	Towpath bank	3·1	1·96 (1·57)	Ro	R	11·7 (58–1)	1·00	—
D 6	Towpath bank under willows	3·5	1·90 (0·84)	Ro	R	—	—	—
D 7	Hedgebank bordering pasture	2·9	1·85 (1·20)	Ro	R	—	—	—
D 8	Willow and alder wood	2·6	2·08 (1·20)	Ro	R	—	—	—
D 9	Stream bank	3·0	2·34 (2·10)	Re–Ro	W–R	14·3 (50–1)	—	—
D 10	Alder wood	2·6	1·68 (1·16)	Re–Ro	P–R	6·2 (32–0)	—	—
D 11	Hawthorn hedge	2·8	2·06 (0·97)	Ro	R	—	—	—
D 12	Alder-willow wood	2·7	2·23 (2·27)	Ro	P–R	16·5 (44–1)	—	—
A 14	Grass bank	4·6	3·11 (0·90)	Er	W	—	—	—
			Open Shaded					
D 13	Willow 'scrub'	3·1	2·36 1·87 (2·23) (1·07)	Re–Ro	W–R	—	1·22	307
A 15	Hedgebank	4·9	3·17 (3·09)	Er	W	16·8 (62–1)	—	—
A 16	Grass bank	4·5	3·69	Er	W	—	—	—
A 17	Grass heath	3·8	—	Er–Re	W–P	—	—	—
A 18	Grass heath	4·9	3·23 (2·43)	Er–Re	W–P	4·6 (18–0)	1·00	—
A 19	Hedgebank at edge of grass heath	4·2	2·62 (1·10)	Er–Re	W–P	—	—	—
A 20	Grass heath	5·3	3·29 (2·23)	Er–Re	W–P	—	1·31	377
D 14	Edge of beech wood	2·7	2·01 (1·65)	Ro	P–R	—	—	—
A 21	Waste ground	4·9	3·82 (2·08)	Er	W	—	—	—
D 15	Stream bank at edge of cultivated field	3·7	3·06 (3·55)	Er–Ro	W–R	—	—	346
D 16	Wood relic	3·0	2·00 (0·42)	Ro	P–R	—	—	—
A 22	Grass verge	4·3	—	Er	W–P	—	—	—
A 23	Grass heath	4·8	—	Er	W	—	—	—

* Er = Erect; Re = Reflexed; Ro = Rolled back. † W = White; P = Pink; R = Red.

population was interesting for it was the only one in which the variety *M. dioicum* var. *albiflorum* was found in any quantity. In this case fully a third of the plants were of this variety. They were responsible for the range of petal colour reported in the table.

The plants growing on the railway bank at Upper Halliford (A3) showed no pink-petalled individuals when this survey was begun. Subsequent to the establishment of the experimental plot about a quarter of a mile (0·4 km.) away, one appeared. All the populations of *M. album* on this (north) side of the river gave averages typical of the species. Nevertheless, one plant was found in the waste mound population (A10) and another in the hedge population (A12) which had the characters of backcrosses of hybrids to *M. album*.

Directly across the river, the willow scrub at Sunbury Lock contained a population of *M. dioicum* (D13) which, apparently, had suffered considerable hybridization and at least one first generation hybrid was recognized, several others being probables. This appeared to be a good example of a *Stage* 2 population. Many plants of *M. album* were to be found lining the path from the road to the lock (A15). Surprisingly, none showed pink petals and, although they appeared to have contributed to the hybridity of the population of *M. dioicum* just described, the converse did not appear to have occurred. Other plants of *M. album* occurred on the towpath bank (A5).

The relation between the populations on the towpath bank at Walton (D4), the ash and oak relic (D2) and Broadwater wood (D3) was of great interest for they represented three stages on a local, ecologically determined xenocline. The population of *M. dioicum* in Broadwater wood (D3) was almost pure. All the characters measured tended to show this and the population was an example of *Stage* 0, for even ecologically neutral characters, such as calyx-tooth length and pollen fertility were typical of the pure species. The ash and oak relic (D2) represented a stage in the deterioration of such a pure population. Serious grass invasion had occurred and the tenancy of *M. dioicum* was threatened. Hybridization with *M. album* had taken place but the effects were not as far-reaching as with the population on the towpath bank (D4). Here the plants were acting as 'woodland indicators'. The condition of this habitat resulted from the making of the Desborough Cut in the early 1930's and since then, at least, extensive hybridization had occurred. Plants of *M. album* existed towards the western end of this population (which was in an advanced *Stage* 2), and plants throughout the rest of the population showed various states of recombination between hybrids and *M. dioicum*. The figures for this population have been separated into two groups (D4 and D4a), consisting of plants with coloured and with white petals, respectively, in order to emphasize the extent of the hybridization of *M. dioicum* apart from any influence on the averages by the white-petalled plants.

D5 represented a population of *M. dioicum* on a bank facing a ditch. Although this was potentially in *Stage* 2, no plants of *M. album* were present and hybridization had not proceeded as far as possible. Further along the River Wey, D6 represented a population related to the previous one. Here a cover of willows had persisted and *Stage* 1 appeared to be represented. D7 was a very small population of *M. dioicum* in a hedge bordering pasture. D8 occurred in a small, damp willow-alder wood and hybridization did not appear to have affected this population very much although a neighbouring population (D9), where the trees had been felled, had suffered quite severely. No plants of *M. album* were present, however, and the only white-petalled plant was a specimen of *M. dioicum* var. *albiflorum*. The cultivated field adjoining contained an obvious first-generation hybrid.

D 10 and D 11 represented the populations of *M. dioicum* in an alder wood and a hawthorn hedge, respectively, at New Haw. Apparently, hybridization had just begun in the former case. The averages for calyx-tooth length and pollen sterility were almost those of the pure species but there were three plants with significantly narrower leaves (leaf-indices 2·41, 2·20 and 2·15) than those of the rest of the population. The two pistillate plants had calyx-teeth of 3·5 and 4·5 mm. respectively, while that of the staminate one was 3·0 mm. together with 32 % pollen sterility. All three plants were strong and appeared to be first-generation hybrids. In the case of the hawthorn hedge population hybridization had occurred on a larger scale as in the alder-willow wood population, D 12.

A 16 was an isolated plant of *M. album*, while plants of this species growing in the grass heath at Seven Hills Road (A 18) contained three probable backcrosses. Similar plants were found in populations A 17 (three plants only) and A 20 which were in grass heath at Burwood Park and Burhill, respectively. A 19 was a mixture of *M. album* with hybrids and occurred on the bank of a half-shaded ditch. Plants of *M. dioicum* remaining in the beech wood at Burhill formed population D 14 and, probably, provided the pollen for the hybridizations in the populations just described. This population was partly in deep shade and partly in the open and as a consequence *Stage* 1 and a potential *Stage* 2 were recognizable. On the banks of a ditch bordering a cultivated field at Norwood Farm, population D 15 occurred. It contained plants of both species together with hybrids and was a very good example of a *Stage* 2 population. *M. dioicum*, still in *Stage* 1, was found (D 16) in an adjoining woodland fragment, while plants of *M. album* (A 21) formed a neighbouring population near the farm buildings. *M. dioicum* was not found again in this area and A 22 represented a population of *M. album* sufficiently removed from the former species to show only one plant with coloured petals. Further south, on the grass heath of Fairmile Common, plants with coloured petals were not encountered.

This series of populations is given in detail because it shows a typical sequence across a region containing the relict species which is surrounded and invaded by a newcomer. Other studies, showing similar results, were made at Trumpsgreen and in the Mickleham and Dorking area (all in Surrey).

(ii) *Brighton to Henfield (Sussex)* (*Fig.* 5)

Along the Dyke Road, leading out of Brighton along the ridge of the chalk downs, typical plants of *M. album* were found commonly (A 1 in Table 2). A 2 and A 3 represented successive populations in the arable fields lying fallow alongside the road leading to Saddlescombe. A 2 contained one pink-petalled plant at the south end of the field among thousands of white ones. At the north end of the field three pink-petalled plants occurred. A 3 was on the opposite side of the road and represented a huge population in which the proportion of plants with pink petals increased gradually throughout in a northward direction. The analyses were made in the northern portion and showed that the pink-petalled plants were of hybrid origin. Plants resembling *M. dioicum* closely in floral characters became especially frequent as the fragment of woodland at the northern end of this field was approached. Plants of *M. dioicum* occurred here and, undoubtedly, provided the pollen for the initiation of hybridization in the greatly expanded populations of *M. album* which resulted from the wartime cultivation and abandonment of the fields. This population of *M. dioicum* (D 1) was in *Stage* 1.

Another population of *M. dioicum* occurred around the base of an elder bush on the

open downland beyond Saddlescombe and above Poynings. This population (D 2) had suffered hybridization which must have been followed by severe selection for, despite a high value for the average leaf-index, there was a relatively small range. All the plants had stout stems, unbranched up to the inflorescence, showing a form resembling *M. album*.

At Poynings a group of populations of *M. dioicum* in *Stage* 1 occurred (D 3–D 5 inclusive) with potential development into *Stage* 2, where lighting conditions permitted. The soils were derived from chalk in the case of D 3 and from Upper Greensand in the cases of
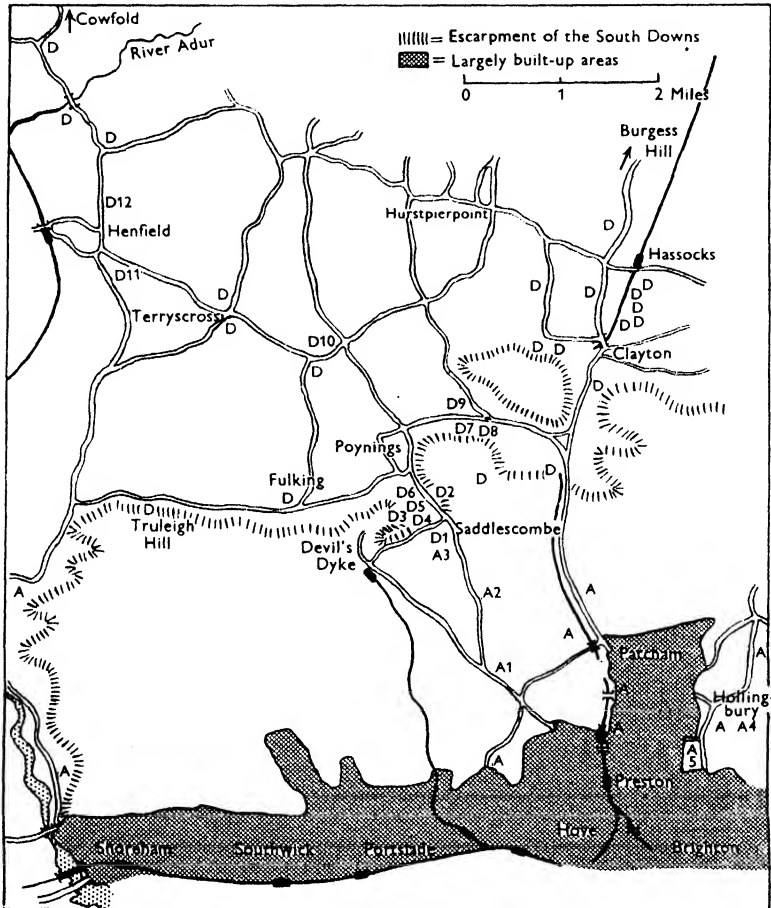
Fig. 5. Map showing the locations of populations of the campions investigated in the Brighton, Henfield and Hassocks area of Sussex. The prevalence of *Melandrium dioicum* upon the Weald and of *M. album* on the chalk downs is shown.

D 4–D 6. D 3 represented the population in a hazel scrub with occasional hawthorns. It had not been cut for many years and the plants were typical of *M. dioicum* in all save ecologically neutral characters. The populations in the ash woods (D 4 and D 5) showed a wider range of characters correlated with the greater light-intensity here and a plant smutted by *Ustilago violacea* was present. Hybridization was marked here and in the population (D 6) lining the path leading from the woods. Despite a wide range of petal colour in the latter, the only white-petalled plant present was a specimen of *Melandrium dioicum* var. *albiflorum*. Nevertheless, the population was virtually in *Stage* 2.

D7 and D8 were populations growing in uncut and cut parts of an ash-elder and hazel wood on the Upper Greensand slope at Newtimber. Hybridization had occurred in both cases but showed in ecologically neutral characters, only, in the shaded habitat. The populations were in *Stages* 1 and 2, respectively. The alder wood at Newtimber (D9) was a *Stage* 1 population containing shade forms, although 'constitutive' characters showed the evidence of hybridization. The cultivated fields adjoining this wood demonstrated

Table 2

Population	Description of habitat	Calyx-tooth length in mm. (grand average of ♂ and ♀)	Leaf-index (range of extremes in parentheses)	Range shown by direction of capsule-teeth	Range of petal colour	Average % pollen sterility (range of extremes in parentheses)	Sex ratio (♀/♂)	Average thickness of ground-leaves (μ)
A1	Waste land by roadside	5·8	3·84 (3·82)	Er	W	14·4 (42–1)	—	—
A2	Cultivated field lying fallow	5·5	3·57 (2·55)	Er	W–P	—	1·46	435
A3	Cultivated field lying fallow*	5·3	3·21 (2·88)	Er–Re	W–P	28·5 (86–1)	0·93	403
D1	Ash, oak and sycamore wood	3·5	1·93 (1·08)	Ro	R	13·2 (32–0)	1·00	—
D2	Under shelter of elder on downland	3·6	2·54 (1·36)	Ro	R	—	—	—
D3	Hazel scrub with hawthorn	3·0	1·68 (0·50)	Ro	P–R	—	1·43	—
D4	Ash wood	3·0	1·64 (0·74)	Re–Ro	P–R	—	—	—
D5	Ash wood (much elder); thinned	3·6	1·69 (1·01)	Re–Ro	P–R	—	—	—
D6	Path bank	4·0	1·97 (2·07)	Re–Ro	P–R	21·8 (67–1)	1·04	325
D7	Ash-elder-hazel wood	2·8	1·83 (0·93)	Re–Ro	P	18·0 (67–0)	1·51	272
D8	Ash-elder-hazel wood; cut	3·1	1·95 (1·61)	Re–Ro	P–R	—	—	310
D9	Alder wood	3·7	1·55 (0·56)	Re–Ro	P	18·1 (69–0)	—	—
D10	Oak wood (*Quercetum roboris*)	2·8	1·71 (0·80)	Ro	P–R	—	2·54	—
D11	Oak wood (*Quercetum ericetosum*)	2·6	1·95 (1·12)	Ro	R	6·0 (33–0)	2·20	—
D12	Oak wood (*Quercetum ericetosum*)	2·9	1·97 (1·05)	Ro	R	—	—	—
*	Plants with coloured petals in A3	5·0	2·99 (2·36)	Er–Re	—	32·8 (86–4)	—	379
*	Plants with white petals in A3	5·5	3·41 (2·88)	Er	—	24·2 (63–1)	—	426

where the original hybrids could have existed even if the vigour of the first-generation hybrids had been insufficient for their growth in the wood. The pedunculate oak wood with hazel coppice known as Shave's Wood contained plants of *M. dioicum* (D10). Here hybridization was not quite so marked as with the previous populations in or near concentrations of *M. album* and a relatively early *Stage* 1 occurred. The two populations D11 and D12 were on the south-east and north sides of Henfield, respectively. *M. album* was not common in this district (on Lower Greensand) and hybridization appeared to be only starting in D11 for the pollen sterility of the twenty-one plants

examined was very low with three exceptions (29, 32 and 33% sterility) and the average length of calyx-teeth was low. D12 showed similar characteristics.

Another transect from Brighton to Hassocks showed a comparable transition from apparently pure populations of *M. album* upon the chalky soils of the South Downs to hybridized populations of *M. dioicum* on the varying soils of the Weald. In this case, however, the Lower Greensand of the Forest Ridge was not reached and the purer populations of *M. dioicum* occurring here were not encountered.

(iii) *Hollingbury and Varndean (Sussex) (Fig. 5)*

A few plants of *M. album* grew around the borders of the playing-fields of Varndean School for Boys, Brighton, before they were ploughed in 1940. This was followed by a tremendous expansion of the population and when the fields were allowed to lie fallow they were covered by a sheet of campions (A5). Pink-petalled plants occurred occasionally and the analyses given in Table 3 show their hybrid origin. The only pink-petalled plant known in this area before the recent war was growing in a bramble-hedge near Hollingbury Camp. With the very favourable conditions resulting from the ploughing at Varndean selection was not severe and forms probably appeared which, otherwise, would have been eliminated. At Hollingbury (A4) there had not been the same expansion and the population was a relict on waste land which was reverting to grass. The population at Varndean cannot be described as being in *Stage* 3 as it is doubtful whether plants of *M. dioicum* ever existed on that land.

Table 3

Population	Description of habitat	Calyx-tooth length in mm. (grand average of ♂ and ♀)	Leaf-index (range of extremes in parentheses)	Range shown by direction of capsule-teeth	Range of petal colour	Average % pollen-sterility (range of extremes in parentheses)
A4	Regenerating downland	6·1	3·32 (2·59)	Er	W	14·8 (69·0)
A5	Cultivated fields lying fallow	4·9	3·69 (3·15)	Er–Re	W–P	*

* Plants with coloured petals 19·7% (66–0). Plants with white petals 8·6% (23–0).

(iv) *Tillington and Petworth (Sussex)*

Near Tillington hybridization was studied in a group of populations in and around arable fields. About 1 km. away, at Petworth, there had been little cultivation of the soil, pasture being the rule. Apparently, a small population of *M. dioicum* in an alder wood had not been hybridized. A large population of the same species in the hawthorn hedges leading from here was potentially in *Stage* 2, but still showed the characters of a *Stage* 0 population with the exception of one plant with highly infertile pollen (60% sterile). Obviously, hybridization had only just begun and the general freedom of this population emphasized that mere felling of woodland does not bring a population into *Stage* 2. Cultivation of the ground must precede invasion by *M. album*.

These investigations show that hybridization between the species has been rife in south-eastern England, much more so than the occasional reports of hybrids in local floras would indicate. Usually, these reports have referred only to plants discovered among populations of *M. album* for here, alone, is there any striking difference in petal colour. In urban areas, both species may be eliminated. According to local information,

less than twenty years ago Barn Hill, Wembley, supported a population of *M. dioicum*. One plant, apparently a backcross of a hybrid to *M. album*, was found when the area was investigated in 1943.

East Anglia

The greatest effects of the invasion by *M. album* appear to have been felt in East Anglia. *M. album* is a common weed throughout the eastern counties, occurring on all soils from the chalk downs of the Gog Magogs and the sandy heaths of Breckland to the fen banks and heavy clay soils of parts of Cambridgeshire and Huntingdonshire. Clarke (1937) remarks upon its especial commonness in fields laying fallow on Breckland.

M. dioicum, however, is rare in Cambridge and Huntingdon and this has been remarked upon with surprise by Tansley (1939). Evans (1939), in his flora of the former county, notes the absence of many common British plants from this county and states that, although the species is locally plentiful just across the Essex boundary, the supposed Cambridgeshire records (at Linton and Bartlow) are erroneous. Nevertheless, Mr H. Gilbert-Carter has told the author (in litt.) that the species exists, in some abundance, in the grounds of Hildersham Hall, within the county limits. Furthermore, the card-index kept by the Cambridge University Natural History Society shows that campions with pink petals have been found in populations of *M. album* at Great Chishall and Great Shelford. It is probable that these were of hybrid origin.

For Huntingdonshire, Dr G. C. Druce, in the Victoria County History, records that the Marchioness of Huntly found the species near Park Cottage at Orton Waterville and that it occurs at Shot Hill. The latter station could not be identified and the former neighbourhood was searched without success. Miss E. A. Baker, B.A., located some pink-petalled specimens at Brampton, near Huntingdon, in June 1942. These were of hybrid ancestry and were growing with plants of *M. album* in two stations at the base of a south-facing hedge in Park Lane. Similar specimens occurred in the New Rectory Orchard, Brampton.

At the suggestion of the author, members of the Huntingdon Wayfarers' Society kept a look-out for specimens during their rambles and Mr Luxton of that society discovered a population of *M. dioicum* in Wennington Wood (vide *Hunts Post*, 29 April 1943). This population was investigated by the author. It consists of a compact and roughly rectangular patch of about 20×15 m. and is mostly under the spread of a single tree of *Quercus robur*. The wood as a whole is a mixture of ash and oak and, in the lighter parts, the shrub- and field-layers are dominated by brambles. Throughout most of the wood, *Mercurialis perennis* is the dominant species of the field-layer accompanied by a varied flora indicative of rather damp conditions (including *Ficaria verna*, *Lychnis floscuculi*, *Hypericum perforatum*, *Filipendula ulmaria*, *Geum urbanum*, *Fragaria vesca*, *Epilobium hirsutum*, *Circaea lutetiana*, *Arctium minus*, *Glechoma hederacea*, etc.). *Mercurialis perennis* is completely absent, however, from the patch containing the mass of *Melandrium dioicum* although there is some mingling at the margins. A list of accompanying species in the centre of the main patch is given in Table 4. In an unshaded space a growth of *Holcus mollis* appeared to have crowded the campions out. Within the main patch the relative light intensity (shade-phase) varied between 7·9 and nearly 100% although mostly nearer the former. The average height of the plants was about 44 cm.

The reason for the extreme localization of the colony was discovered in the soil conditions. Throughout most of the wood the soil was derived from the heavy clay which is

typical of this region. There was only a little leaf litter above the soil surface and the humus layer was very thin. Almost coincident with the area of the campion colony there was an abundance of rotting wood forming a layer varying in depth from 1 to 5 cm. above the clay and the plants were most prolific where it was deepest. Table 5 shows a comparison of samples taken in the top 5 cm. of the soil from each of the situations mentioned (three samples *A*, *B* and *C* being taken at different spots in the main colony in order of decreasing depth of the layer of rotting wood). A region of light, well aerated though damp soil was provided and most of the very shallow root systems of the plants were found in the wood-layer, their tap-roots tending to run horizontally along the top of the clay.

Table 4. *Species accompanying* M. dioicum *at Wennington Wood, Hunts*

Percentage frequency determined by the use of twenty-five 0·1 sq.m. quadrats

Species	Percentage frequency
Scilla non-scripta	60
Rubus fruticosus (agg.)	52
Glechoma hederacea	44
Poa nemoralis	24
Ficaria verna	20
Geum urbanum	20
Fragaria vesca	20
Holcus mollis	20
Viola riviniana	8
Veronica hederifolia	8
Epilobium hirsutum	4
Rumex nemorosus	4
Agrostis tenuis	4

Table 5. *Analyses of soil samples taken from Wennington Wood, Hunts*

pH determined colorimetrically

	pH	Loss on ignition (percentage of dry weight of soil)
Melandrium dioicum society:		
A (see text)	6·0	19·0
B	6·0	13·4
C	6·2	13·0
Mercurialis perennis and *Melandrium dioicum* outliers	6·4	11·1
Mercurialis perennis society	6·6	12·0

The plants in this population were all semi-shade forms with relatively unbranched stems. Measurements of the length of calyx-teeth and the thickness of leaves from the ground-rosette showed the population to be very free from hybridization with *Melandrium album*.

Wennington Wood is a portion of the original forest which, during the reign of King Henry II, covered North Bedfordshire and Huntingdonshire to the borders of the Fens near Ramsey (Rodgers, 1941), and the characters discussed above indicate that this 'island' population is a relic which has maintained itself only because of the peculiarly favourable conditions found at that spot. The purity of the population is related to the absence of *M. album* from the immediately surrounding arable land. Brampton Wood is another relic of the primeval forest and the pink-petalled specimens from Brampton may have been derived from another relict population. The pink-petalled campions from Cambridgeshire would appear to represent an even later stage in the disappearance of *M. dioicum* and its absorption into *M. album*. Such a disappearance is likely to be due to a combination of factors but the possibilities may be considered separately.

One characteristic of this area is its low annual rainfall; that for Huntingdon averaging about 549 mm. (average for 1881–1915, see *British Rainfall*, 1939) and that for Cambridge

about 534 mm. (loc. cit.). The warm, dry summers make drought common in this season. The combination of this climate with the poor, sandy soil of Breckland suffices to explain the absence of *M. dioicum* from that particular district, even though it may have been present at the time when Breckland was naturally afforested (vide Farrow, 1925 and Godwin, 1944). Over the whole of the two counties, however, there are local areas damp enough to support the species and one would hardly have expected such nearly complete absence. Furthermore, the existence of the population in Wennington Wood shows that *M. dioicum can* exist with the rainfall which obtains there, although browning and dying of the foliage was witnessed by the middle of July.

This part of East Anglia is often subject to severe frosts in late spring and Watt (1936), in a study of Breckland, has shown that young bracken fronds and even rhizomes to a depth of 10 cm. have been killed as late as the beginning of June. The work of Åkerlund (1933) has shown that *M. dioicum* is susceptible to frost injury and that this is related to the over-wintering buds being situated above ground. It is possible that this factor might be responsible for occasional considerable mortality of plants growing in this region, especially such as might be left unprotected by the felling of trees. However, Mr H. Gilbert-Carter has pointed out that the species survives and seeds itself in the Cambridge University Botanic Gardens and Bateson (1913) has mentioned the same fact. Before the discovery of the population in Wennington Wood a transplantation and seed-sowing experiment was carried out from Walton, Surrey, to a cleared patch in the orchard owned by Mrs Cranfield of Huntingdon. The plants which were established in 1942 were still healthy in 1945. Although experiments of this sort, which do not reproduce natural conditions completely, cannot be conclusive, the appearance was that *M. dioicum* would not be ousted by climatic conditions alone.

As Evans (1939) remarks, the absence of the species is hardly likely to be due to the lack of a suitable soil as Cambridgeshire provides a considerable variety. Nevertheless, large portions of this county and of Huntingdonshire are covered by heavy soils derived from boulder clay, Oxford clay, Ampthill clay and silt. Such soils are not those upon which *M. dioicum* can best endure competition (vide Baker, 1945, 1947a).

It seems that the fundamental cause of the disappearance of the species is the deforestation of the area and its conversion to agriculture which has facilitated the establishment of *M. album* in the area. Recently, Godwin (1944) has shown that the Breckland heaths originated from a pre-existing vegetation of closed mixed oak forest and offers strong evidence that a clearance took place in Neolithic times. Reference has been made, already, to the large forest which once covered Huntingdonshire and 'Wabridge Forest' is shown on early seventeenth-century maps as lying just north of Huntingdon (Rodgers, 1941). By 1910 more than two-thirds of the area of Cambridgeshire and over half of Huntingdonshire were occupied by arable land while the only extensive re-afforestation upon the sandy heaths has been with conifers.

M. dioicum has been known to linger on in other areas after deforestation as a 'woodland indicator', but it appears to be intolerant of grass competition and ploughing and in this case the contributory factors of drought, frost and uncongenial soil have speeded its disappearance. The spread of agriculture introduced habitats unsuited to *M. dioicum* but very suitable for *M. album* which, because of its preference for almost 'continental' conditions and its capability of flourishing upon a wide range of soils, has become exceedingly common. Undoubtedly, the increase of this species has resulted in widespread

hybridization and in the resulting populations the advantageous characters of *M. album* would be expected to be selected and the last obvious remnant of the previous occupation of the area by *M. dioicum* would probably be the occurrence of pink-petalled plants among the populations of *M. album*. Except for the populations at Wennington Wood and Hildersham Hall this (*Stage* 3) would appear to have been reached in Cambridgeshire and Huntingdonshire.

THE FUTURE OF THE SPECIES

The history of the two species in this country is unfinished. The spread of *M. album* at the expense of *M. dioicum* is bound to continue along with the increasing cultivation and urbanization of the countryside. The effect of the recent war, especially, has been marked throughout the country. With the construction of camps (the use of woodlands being favoured) and of aerodromes, the damage to the countryside caused by heavy vehicles and the creation of waste-land by bombing, the increased provision of suitable sites is bound to result in increased colonization by *M. album*. The vast increase in agronomy during the war years has had a very great effect. The ploughing of pasture and parks has opened ground to colonization by *M. album* where it was unable to compete with the grass previously. The sheets of plants of this species to be seen in fields which have been ploughed on the South Downs and, subsequently, allowed to lie fallow, indicate that the species has not been slow in following opportunity, here, where the soil is particularly favourable.

Although climatic conditions elsewhere in the British Islands are unlikely to be as favourable for the complete replacement of *M. dioicum* by *M. album* as those in East Anglia, the prophecy may be made that this condition will generally be reached over the major part of the country that is considerably farmed although, in more oceanic regions, the equilibrium might be expected to rest with a different combination of characters.

THE CAMPIONS IN NORTH AMERICA

In contrast to the conditions in Europe, those in America may be considered. Here neither species is indigenous. John Bartram (1699–1777) worked with campions in Pennsylvania but it is clear that his material was imported from England (vide Zirkle, 1935). Early floras of the U.S.A. make no mention of either species and even in 1888 a *Catalogue of Canadian Plants* (Macoun, 1888) contains no reference to the species. Gray (1895–7, vol. I, p. 227) refers to both species in detail and remarks upon the likelihood of there being naturally occurring hybrids, as the species were '...not always clearly distinguishable, notwithstanding the rather conspicuous differences exhibited by the extreme forms'.

Subsequent floras record the gradual spread of both species from their points of introduction into the eastern states. They now occupy an extensive area in the eastern and north-central states of the U.S.A. and in southern Canada. Muenscher (1935) has added the Pacific north-west to the territory occupied by *M. album* and there is a specimen in the herbarium at Kew from a sandy beach 14 miles east of Nome, Alaska (collected by C. W. Thornton, August, 1937). *M. dioicum* appears to have been the more frequent (or more often noticed), originally, but it has not paralleled the spread of *M. album* which is becoming increasingly common, although there is a specimen from Vancouver (see p. 116).

The campions were introduced through the agency of impure clover seed (Kay & Lees,

1913) and in the rubbish from grain-ships added to the ballast heaps of Philadelphia (Martindale, in Ridley, 1930). There is no evidence in favour of the belief (Hultén, 1937) that *M. album* survived the last glaciation in eastern North America. The rapid spread of the species appears to have been largely through the sowing of impure clover and alfalfa seed. The habitats occupied by the two species in America are similar to those inhabited by *M. album* in Great Britain, viz. meadows, fields, ballast and waste places for *M. dioicum* and grasslands, new clover and alfalfa seedlings, cultivated fields, waste places, ballast (especially along railroads) and roadsides for *M. album*. In the available literature there is no record of either species from any natural habitat or from woodland. The specimens of *M. dioicum* from Garrow Bay, Vancouver (collected by M. M. Whiting and K. J. Stewart, 28 April 1935) must be atypical in their habitation of a woodland situation. They are of a shade form with rounded leaves but the calyx of one resembles that of *M. album*.

The means of introduction and habitats occupied by the species raise grave doubts as to whether the material with coloured petals is not, in fact, of hybrid ancestry. It has been shown (Baker, 1945, 1947 *a*) that *M. dioicum* rarely, if ever, occurs as a weed in this country and seed coming from cultivated land is much more likely to be from plants of hybrid ancestry. For certainty, typical plants of this species would not be able to endure life on ballast heaps and waste places, in cultivated fields and with the competition of grasses in meadows. With the thrusting of the two forms into a similar range of habitats further hybridization is an unavoidable consequence. Forms least resembling *M. dioicum* as it is known in Europe are bound to be selected.

The descriptions of '*M. dioicum*' given by the authors of various American floras contain a number of features reminiscent of hybrids. On the other hand, Gray (1895–7), who mentioned the intergradation, describes the extremes in terms which are perfectly typical for pure-bred plants and could represent extreme segregants. Shull (1910, 1912, 1923, etc.) has bred a large number of the progeny of red- and white-petalled plants (which he calls, collectively '*Lychnis dioica*') from stations mostly in America. He has made his conclusions perfectly clear (1923, p. 223): 'All of these forms—of whatever name and wherever collected—bred together without any diminution of fertility—in fact usually with increased fecundity; and, although there were numerous differentiating hereditary characters, these were not grouped in the wild forms in such a manner as to make it profitable or convenient to attempt to keep track of specific distinctions, as such, in the experimental garden. In my published accounts of these experiments the Linnean designation, *Lychnis dioica*, was the only one which could be usefully employed, the English forms *L. diurna* and *L. vespertina* and the German forms *Melandrium album* and *M. rubrum* being incapable of maintenance.' Shull maintained this attitude in 1940 (vide Warmke & Blakeslee, 1940), and his genetical results do appear to substantiate his statements. Western European geneticists, however, have not been troubled in the same way. Even though they may unite them into one species (cf. Löve, 1944), they are quite certain of the distinctness of the forms (cf. also, Rolfe, 1900; Winge, 1927; Åkerlund, 1933; Baker, 1945, 1947 *a*; and many others).

Jensen (1940) does not believe in the existence of sex-chromosomes in *M. album*. His arguments are based upon meiotic irregularities in the American material which he has examined. He refers to the great deal of imperfect pollen produced by the plants and to the several 'diagnostic hybrid characters' which are present in the species and point to

previous hybridization as the cause of the irregularities and the 'false appearance of sex-chromosomes'.

There can be little doubt that the two separate species do not exist in America and that in the balance of characters plants more nearly resemble *M. album* than *M. dioicum*. In opposition to the condition in Europe, where one of the pure species originally inhabited woodland, extreme segregants from the hybrid complex probably are alone in inhabiting this community in America. The existence of this hybrid swarm must have resulted from the particular means of introduction of the species and their being thrust into the same ecological niche. The species may be said to have *begun* their colonization in *Stage* 3 (see p. 98) in contrast to the condition in Europe where this stage is only being reached gradually. The future of the species in America may well be different from that in Europe and is likely to repay first-hand study.

SUMMARY

1. A theoretical analysis of the invasion of an area already containing one form by another, closely related form is presented. Four distinct stages are envisaged:

(i) The original condition (*Stage* 0).

(ii) If the forms are inter-fertile, the introduction of characters which are neutral as far as the ecological distinction between the forms is concerned (*Stage* 1).

(iii) Following a modification of the environment, the introduction of characters excluded previously on ecological grounds (*Stage* 2).

(iv) The disappearance of the original form except for neutral characters (*Stage* 3).

Such a sequence may occur in one place through a period of time or at the same time over a wider area. A *xenocline* is defined as a cline of hybridization following the spread of the immigrant form from its place of introduction. Xenoclines may exist in forms corresponding with topoclines and ecoclines, respectively.

2. The general relationships of *Melandrium dioicum* and *M. album* are discussed. *M. album* is shown to have arisen by ecogeographical divergence from an ancestor probably resembling *M. dioicum* quite closely, and the two species form relatively fertile hybrids.

3. The fossil and historical records show that *M. dioicum* colonized northern Europe and the British Isles by natural means and that, subsequently, *M. album* has spread as a follower of agricultural man.

4. Suitable criteria of hybridity for the campions are enumerated.

5. Using the characters determined to be suitable, field observations made in Wales, south-eastern England and East Anglia are described.

(i) In western Wales, populations of *M. dioicum* are still mostly in *Stage* 0.

(ii) In south-eastern England, all stages may be found and populations of *M. dioicum* appear as island relics largely surrounded and invaded by a network of *M. album*.

(iii) In East Anglia, the opposite extreme to the Welsh condition has been reached. Over most of Cambridgeshire and Huntingdonshire forest-clearance followed by agronomy and coupled with unfavourable climatic and edaphic conditions has resulted in the almost complete disappearance of *M. dioicum*. Only one certain and one probable relict population are known in the two counties. *M. album* has found extremely favourable conditions, has become well established and has helped to speed the disappearance of *M. dioicum*.

6. The probable future of the two species in the British Isles is discussed.

7. Conditions in Great Britain are contrasted with those in America, where it appears that hybrid material was introduced along with *M. album* and the populations of campions are heterogeneous from the start.

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A SURVEY OF THE ROCKLAND-CLAXTON LEVEL, NORFOLK

By J. M. LAMBERT, *Westfield College, University of London*

(With one folding figure and seven Figures in the Text)

The following short paper is the outcome of part of the ecological work carried out, under direction, by a number of graduate and undergraduate students of Westfield College* during two short expeditions to Norfolk in the summers of 1946 and 1947. The work consisted in the main of a detailed survey of the present vegetation of the Rockland-Claxton Level, together with some investigation of the soils and drainage conditions; and although evidence is not yet available for the interpretation of the complete vegetation map constructed, some of the results already obtained appeared to be of sufficient interest to be recorded here.

A. INTRODUCTION

In an earlier paper (Lambert, 1946), the fenland of the Surlingham-Rockland peat basin was differentiated into (i) the primary areas, where active development is still taking place, and (ii) the secondary anthropogenic fen: the latter was further subdivided into (a) the unembanked 'mowing-marsh' areas served by dykes with free circulation of tidal (but non-brackish) water, and (b) the embanked grazing areas in which the water-level in the dykes could be artificially lowered by pumps or sluices. The extent and relative distribution of these areas is shown in Fig. 1; and it will be noted that, whereas the embanked areas in the vicinity of Surlingham Broad are now entirely derelict, the Rockland-Claxton Level south of Rockland Broad is still maintained as rough pasture.

Pending further evidence, a consideration of the vegetation of the embanked areas was purposely omitted from the earlier account (Lambert, 1946, pp. 250-1). This later survey of the Rockland-Claxton Level, undertaken partly as a useful ecological exercise in team work and partly for the intrinsic value of any results obtained, has furnished a certain amount of information which can now be considered in relation to the areas previously described.

B. GENERAL DESCRIPTION OF THE LEVEL

(i) *Historical*

No information has yet been obtained as to the approximate time at which the area was first embanked, but it is probable that the original banks were gradually raised and made more efficient during the last century. Mr C. R. Cadge, of the Lower Yare Second Internal Drainage Board, writes that 'Prior to what is known in this part of the country as "the great flood of 1912", I believe all the Rockland Marshes were of real value and good grazing land, but they have never recovered since that flood'. The Minutes of the Claxton and Rockland St Mary Drainage Board (1919-37) show that after the 1914-18 war a considerable amount of repair work to the drainage system and embankments was carried out, but, despite this, in 1928 serious consideration was given to the economic advisability of allowing the Level to become completely derelict. Nevertheless, some degree of pumping was continued, although drainage was made increasingly difficult both

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* The following students participated in the work: S. Barkley, J. Bremner, H. Bristow, S. Cole, C. Humphreys, M. Parker, H. Shields, P. Tizard, E. Uren and D. Williams.

by progressive lowering of the general surface of the Level through peat wastage, and by the greater tidal upflow in the main river (caused by dredging operations and the opening of the wider New Bridge at Yarmouth in 1930). At the time of the survey, however,
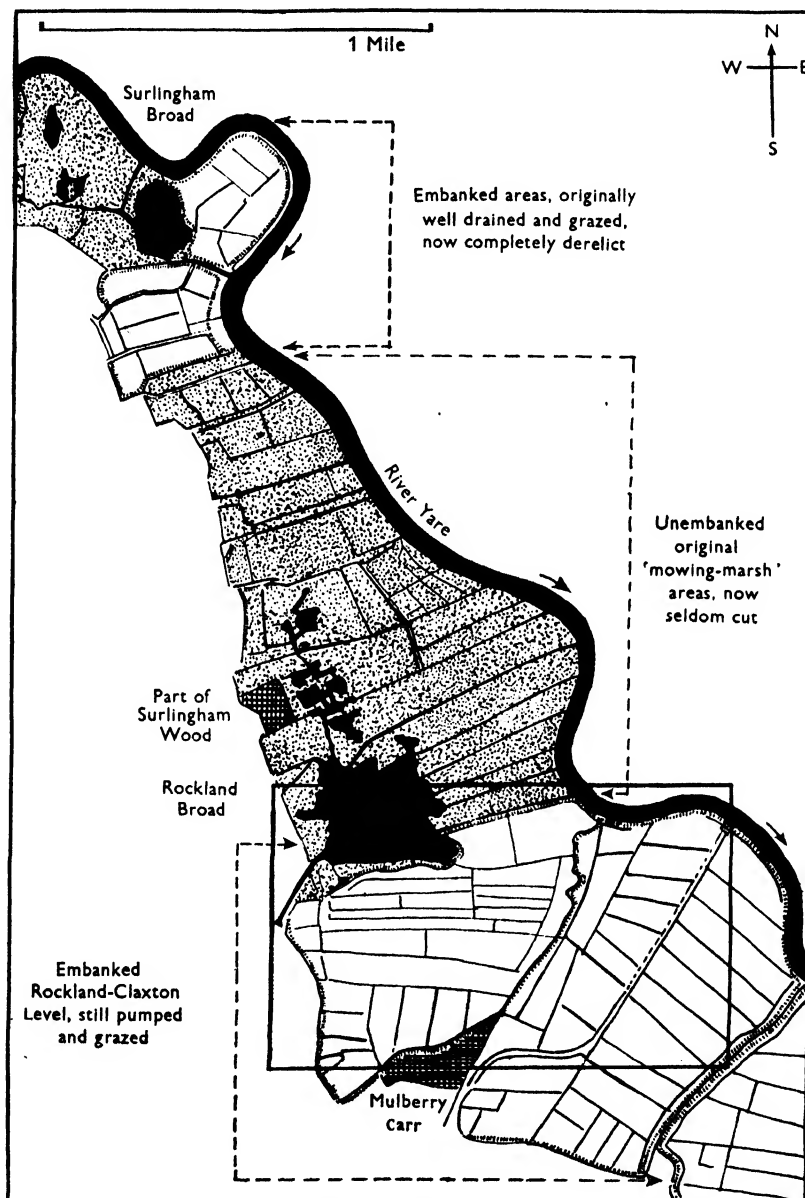
Fig. 1. Map showing the relationship of the embanked areas (plain) to the unembanked primary fen and 'mowing-marshes' (stippled) in the Surlingham-Rockland peat basin. The area discussed in detail is enclosed in a rectangle.

a much more serious attempt was being made to restore the value of the Level by embankment repairs and cleaning of dykes, and in 1947 a new pumping station was under construction to replace the original oil turbine pump.

(ii) *Present drainage system (see Fig. 2)*

The Level is intersected by a number of interconnected dykes, the majority of which were badly overgrown until several of them were cleaned and widened within the last 3 years. In addition to the artificial dykes, the Level is traversed by Claxton Fleet, originally the bed of a small sluggish tributary stream arising in the surrounding upland. This has a low embankment on its east side, and appears to have opened to the river in the past by a sluice; but the upland water is now deflected, and the original channel of the Fleet incorporated into the general network of the drainage system so that its independence is lost. A derelict sluice is further situated at the south-east corner of Rockland Broad, between areas 1 and 3, at the original opening of a now overgrown branch of the Fleet.
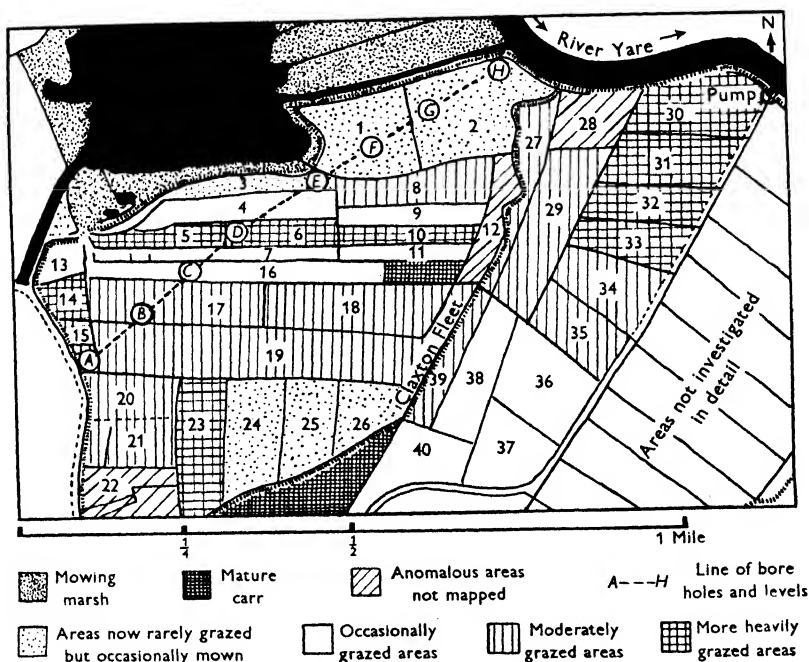

Fig. 2. Key map to the area surveyed.

The water-level in all dykes is ultimately controlled by the Claxton pumping station (Fig. 2, extreme north-east), but the obsolete oil pump proved inadequate to cope with the total body of water involved, with the result that up to the time of the survey much of the area was water-logged throughout the winter. The wettest parts (areas 1, 2 and 3) lie adjacent to Rockland Broad and its dyke, where there has been recurrent trouble with seepage of water through the embankment to the Level.

(iii) *Present utilization of the Level*

The major part of the Level still appears to be subject to fairly widespread though intermittent summer grazing, especially by young stock. Evidence accumulated both by inquiry and by observation during the survey showed some variation in intensity of grazing over the Level as a whole, and this is indicated in general outline in Fig. 2.

A few areas, shown by stippling in Fig. 2, are now rarely grazed at all, though they are very occasionally mown. In many of the well-grazed areas, also, the taller stock-resistant vegetation is sometimes mown for litter towards the end of the summer.

Areas 12 and 28, which bear a somewhat different vegetation from the rest of the Level, were suspected of having been ploughed and seeded at some earlier period, and were omitted from the general survey.

(iv) *Edaphic considerations*

Apart from the characters already mentioned, the Level has a further especial interest in its general relationship to the Surlingham-Rockland peat basin as a whole. A very significant map, originally published by Pallis (1911) and reproduced here as Fig. 3, shows that the lower Yare valley can be divided into three regions, with the substrate consisting successively of (*a*) peat, (*b*) 'ooze' or clay, and (*c*) 'loam' or silt. It will be seen from this figure that the Level is situated partly within the clay region and partly upon peat.
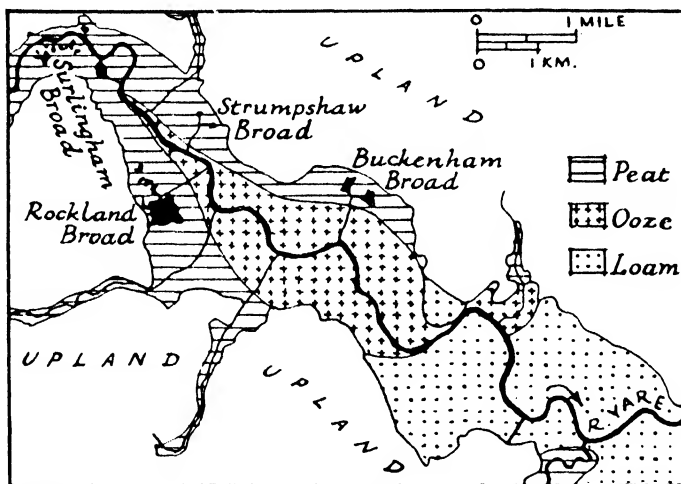

Fig. 3. Part of the Yare valley, showing the relative distribution of peat, clay (ooze), and silt (loam). (Reproduced from Tansley, 1939, after Pallis, 1911.)

The clay tongue running up the Yare valley appears to be essentially comparable to similar clay wedges found by J. N. Jennings of the Department of Geography, University College, Leicester (1939 and 1947, unpublished) to occupy the lower reaches of the Bure and its tributary, the Ant. This clay is thought to be estuarine or lagoon in origin, representing deposits formed by a marine transgression over earlier valley peats. In the 'mowing-marsh' areas above Rockland Broad it is covered by nearly a metre of peat formed after the retreat of the sea, but in the embanked and drained areas wastage of this superficial peat has reduced the surface of these areas almost to the level of the clay itself. This lowering of the surface was well illustrated by a line of levels taken across the drained Rockland-Claxton Level (Fig. 2 *A–H*), which gave values below Ordnance Datum (Newlyn) for points *D–H*, with a maximum depression of -0.30 m. at point *E*. An extension of the levelling line northwards from point *H* (-0.04 m.) to a corresponding point on the adjacent undrained 'mowing-marsh' showed the latter to be 0.85 m. higher, with an absolute value of $+0.81$ m. O.D.

Although in a few patches of the Rockland-Claxton Level the surface peat is sufficiently wasted to expose the clay below, over the major part of the area the latter is still covered by several centimetres of structureless mouldered peat. The approximate lateral boundary between the clay and the main mass of the peat was therefore traced by means of a rough hand analysis of samples taken at a depth of 25 cm. at a number of points over the area. The soil map constructed from these observations is illustrated by Fig. 5, and a dotted line is inserted to represent Pallis's original delimitation of the boundary, as far as could be judged by reference to her map.

The figure shows that some admixture of clay extends further towards the valley margin than originally estimated.* The line of the boundary is moreover to some extent modified by the presence of the Claxton Fleet, originally a small tributary opening into the Yare, and hence probably the seat of invasion by a lateral tongue of clay. In addition, the Fleet probably carried down a certain amount of inorganic material from the uplands, which would become admixed with the peat along its margins. The pure peat substrate is therefore restricted to a relatively small area immediately south of Rockland Broad, and even here the marginal samples were found to contain a certain proportion of landwash sand derived from the Norwich Crag which borders the valley in this part.

In order to investigate more fully the vertical as well as the horizontal relationship between the clay and the peat, a line of bores (Fig. 2 *A–H*) was put down across the Level, extending approximately from the valley edge to the river bank. The section obtained is represented by Fig. 4. The detailed interpretation of this section, which accords very well with unpublished sections obtained by J. N. Jennings in the Ant and Bure valleys, will be left for discussion elsewhere; its main purpose here is to indicate the interdigitation of the clay wedge between the earlier valley peats and the thin layer of wasted surface peat, and the wedging out of the clay towards the valley margin. An incidental feature of interest in the section is the thin layer of greenish yellow nekron mud obtained in Bore *C*, rich in fresh-water shells and undoubtedly representing the former southward extension of the open water of Rockland Broad.

C. The Vegetation of the Level

Since the degradation of the Level as pasture following the 1912 flood, and the frequent water-logging of the area resulting from inadequate drainage, the smaller pasture plants assumed to have been predominant originally have undoubtedly been replaced progressively by more typical marsh and fen plants. It has been noted (p. 121) that the Level is at present in process of subjection to a more extensive reclamation scheme, but at the time of the survey this was not sufficiently advanced to have had any significant effect on the vegetation; on the other hand, the imminence of these operations gives added importance to the vegetation survey carried out at this particular time, since a basis is now provided from which subsequent modifications of the vegetation may be followed in relation to the improved conditions.

The complete vegetation map constructed to show the distribution of the dominants is too complex to reproduce here in its entirety. However, a general idea of the relative distribution of the main species over the Level may be obtained from Table 1, which summarizes data obtained from 115 metre quadrats made at representative points. These

* *Note.* The apparently anomalous peat symbol in area 37 is due to the occurrence here of the upper limit of the clay at a depth of 33 cm. instead of within the first 25 cm. as was usual.
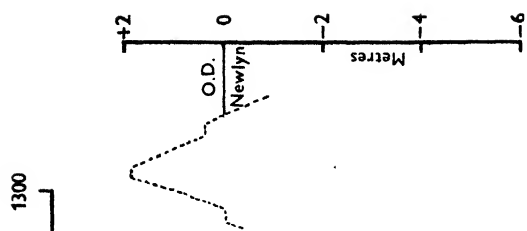
1300

+2

0

O.D.
Newlyn

−2

Metres

−4

−6

Table 1. *Table indicating the relative constancy of the main species of the Rockland-Claxton Level under different edaphic and biotic conditions*

Legend — Percentage constancy of species in quadrats:
- Under 10%
- 10–20%
- 20–30%
- 30–40%
- 40–50%
- Over 50%

	Nature of substrate				Present economic status			
	Peat and landwash sand	Peat predominant	Peat and clay admixture	Clay predominant	Practically ungrazed —occasionally mown	Lightly grazed	Moderately grazed	More heavily grazed
No. of quadrats employed	12	30	53	20	19	30	40	26

Species occurring predominantly on peat substrate:
- Lysimachia vulgaris
- Thalictrum flavum
- Prunella vulgaris
- Iris pseudacorus
- Rhinanthus crista-galli
- Galium uliginosum
- Vicia cracca
- Briza media
- Parnassia palustris
- Phragmites communis
- Molinia caerulea
- Lotus uliginosus
- Festuca elatior
- Juncus inflexus
- Triglochin palustre
- Potentilla erecta
- Hydrocotyle vulgaris
- Ranunculus acris
- Galium palustre
- Juncus subnodulosus
- Filipendula ulmaria
- Plantago lanceolata
- Carex flacca
- Ranunculus repens

Species occurring predominantly on clay substrate:
- Cardamine pratensis
- Poa trivialis
- Bellis perennis
- Phalaris arundinacea
- Glyceria fluitans
- Carex acutiformis
- Alopecurus geniculatus
- Glyceria maxima
- Equisetum palustre
- Polygonum persicaria
- Rumex acetosa
- Taraxacum officinale
- Lolium perenne
- Agrostis stolonifera
- Juncus effusus var. compactus
- Festuca rubra
- Holcus lanatus
- Potentilla anserina

Marginal species:
- Pulicaria dysenterica
- Mentha aquatica

Species indifferent to substrate:
- Eupatorium cannabinum
- Angelica sylvestris
- Lythrum salicaria
- Cirsium palustre
- Cynosurus cristatus
- Cerastium vulgatum

Increasing tolerance or resistance to grazing →

Note. Species occurring in less than 5% of the quadrats are omitted altogether; species which are also prominent in the 'mowing-marsh' areas are italicized.

quadrats are too few and are not sufficiently randomized to the results to have much value from a statistical point of view, but nevertheless they serve very well to indicate certain features of interest.

In Table 1, the quadrat data are classified on very general lines in relation to the two major factors affecting the vegetation, i.e. the nature of the substrate and the intensity of grazing. It should be noted that the table indicates only the relative *constancy* of the species over the area, which does not necessarily bear a direct relation to their relative *abundance*.

In many parts the Level is at present dominated by species which form prominent constituents of the 'mowing-marshes' to the north. The three main species of the latter were found to be *Glyceria maxima*, *Phragmites communis* and *Juncus subnodulosus* (Lambert, 1946). It was suggested there that the observed limitation of *Glyceria* to areas supplied by circulating non-brackish tidal water, or else to predominantly inorganic areas at the edge of the peat basin, could be related primarily to its mineral requirements, while the less exacting *Juncus subnodulosus* occupied the centre of the peat strips; *Phragmites communis*, with apparently intermediate mineral requirements, appeared less tolerant of summer cutting than the other two species, but tended to encroach upon both in areas where cutting had been relaxed. Since these three species are all present in varying abundance in the Rockland-Claxton Level, it seems appropriate to consider first how far their observed distribution here accords with the ideas already advanced.

The present general distribution and abundance of these species is indicated in Figs. 6–8. It is at once apparent that *Juncus subnodulosus*, which is perhaps the most limited of the three on the unembanked 'mowing-marshes', is here on the contrary the most widespread and ubiquitous, and in fact dominates extensive stretches of the Level. On the other hand, *Phragmites*, which forms the most prominent constituent of the more neglected 'mowing-marshes', is here greatly restricted in its distribution.

Juncus subnodulosus, although to some extent attacked by grazing stock, nevertheless appears to be avoided when other pasture plants are available, and hence it is not surprising that it should have become so abundant over a large part of the Level. Table 1, however, shows that it is less constant in the most heavily grazed areas than in the others; moreover, notwithstanding its ubiquity, Fig. 6 shows a definite diminution in its abundance towards the clay areas (where as a stock-resistant species it is largely replaced by *J. effusus* L. var. *compactus* Hoppe), and it is still more sparse on the shallow peat overlying inorganic material at the valley margin in areas 13–15, 20 and 21.

On the other hand, *Glyceria maxima*, which shows no marked difference in constancy between mown and grazed areas, shows an interesting inverse relation to *Juncus subnodulosus* with respect to the soil conditions. Though rarely attaining dominance over any extensive area, it is nevertheless most conspicuous on the clay areas and towards the inorganic valley margin, but in the pure peat areas is restricted to a few patches occurring mainly in the vicinity of the dykes.

In contrast to *Juncus* and *Glyceria*, the limited distribution of *Phragmites* appears to be far more controlled by biotic factors than by the nature of the substrate. It is obvious from a comparison of Fig. 8 with Fig. 2 that its presence in any abundance (i.e. in areas 1–3 and 24–26) can be very closely correlated with absence of grazing irrespective of whether the substrate of these areas is predominantly peat or clay, and that its sparseness over the grazed areas is similarly independent of soil conditions. This is perhaps most strikingly illustrated by a comparison of areas 23 and 24.

The relationship of *Juncus*, *Glyceria* and *Phragmites* to each other within the Level was observed to be to a large extent independent of slight variations in drainage conditions resulting from minor differences in surface levels of the various areas and in degree of

● Clay predominant in substrate   ◑ Peat-clay admixture—proportions variable
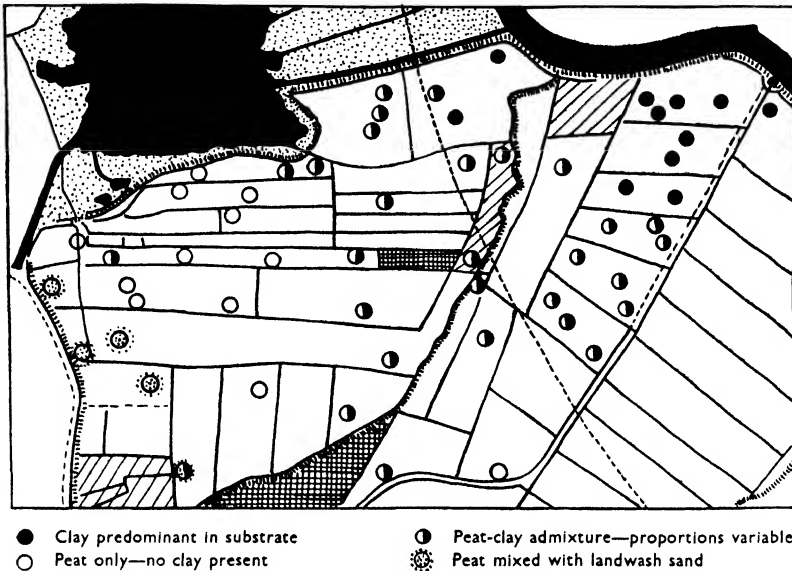○ Peat only—no clay present   ⊛ Peat mixed with landwash sand

Fig. 5. Position and rough qualitative analysis of soil samples taken at a depth of 25 cm. over the area. (The dotted line represents approximately Pallis's original estimation of the boundary between the peat and clay.)

Fig. 6. The distribution of *Juncus subnodulosus* over the area.

overgrowth of the dykes. All three species have a fairly wide vertical range in relation to the water table, and the variations observed fell well within this range. In the unembanked 'mowing-marshes', the importance of dyke overgrowth is exaggerated because of its effect on the circulation of tidal water, but in the embanked Level, where the dykes act

more as sumps, and where in any case there is widespread water-logging except at the height of summer, this factor is minimized.

To sum up therefore the distribution of these three species within the area at present under consideration, it seems that, although at first the ecological conditions obtaining appear to be very different, in effect an essentially similar relationship exists between them
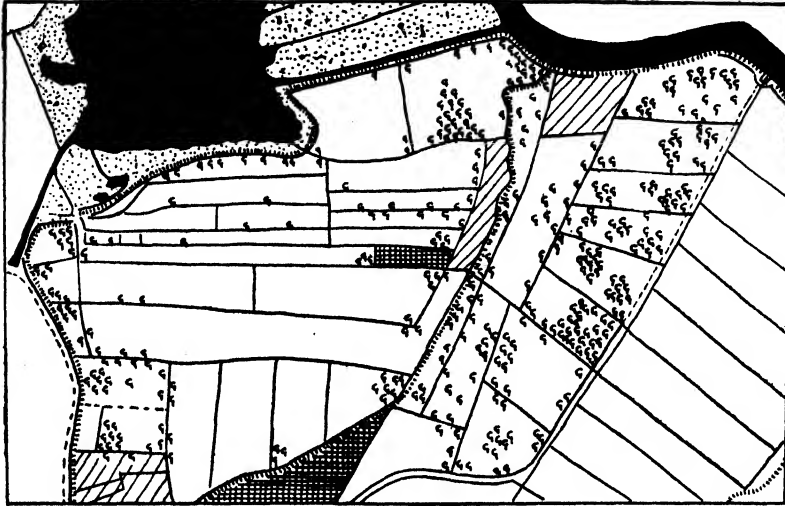
Fig. 7. The distribution of *Glyceria maxima* over the area.
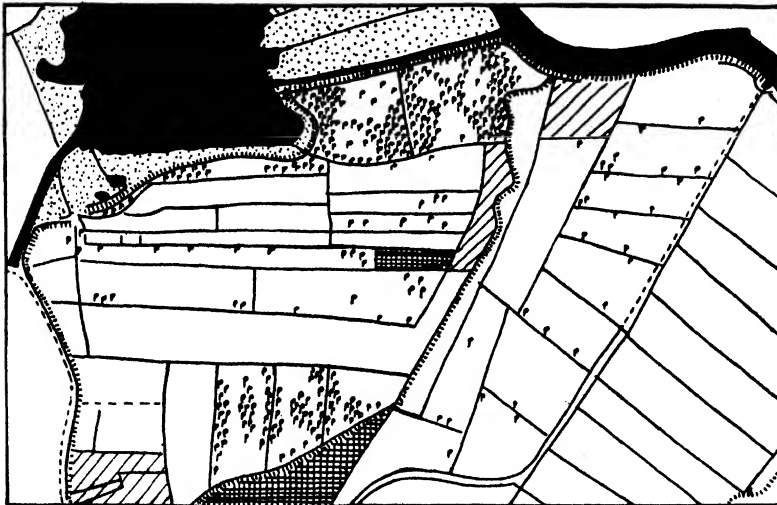
Fig. 8. The distribution of *Phragmites communis* over the area.

as in the 'mowing-marsh' areas of the secondary fenland. In the latter, the major differentiating factor operating between *Juncus* and *Glyceria* is presumed to be the renewal of mineral supply by circulating tidal water. Within the Level, such tidal water is excluded altogether, with an accompanying increase of *Juncus* and decrease of *Glyceria* (which is probably also to some extent a result of differences in resistance to grazing); but in the clay

areas and towards the valley margin, where the predominantly inorganic substrate might be expected to provide some compensation for the loss of minerals brought by tidal water, *Glyceria* becomes relatively abundant (with a corresponding diminution of *Juncus subnodulosus*) even on the more intensively grazed areas (such as areas 30–33). In contrast, *Phragmites* appears even less resistant of grazing than of summer mowing, and hence is of very restricted distribution; but once this limiting factor is removed, it can apparently hold its own with both *Juncus* and *Glyceria*, and, given time, would probably overrun them both irrespective of the nature of the substrate.

A more general impression of the main similarities and differences between the vegetation of the Level as a whole and that of the 'mowing-marshes' may be gained from a comparison of Table 1 with the table of 'mowing-marsh' species previously given (Lambert, 1946, pp. 260–1). Any *close* comparison of these two lists must automatically be ruled out by differences in the methods employed for constancy estimations and in the basis for grouping of the species in the two cases (such differences being inherent in the nature and purpose of the respective surveys); but in order to equate the two lists as far as possible, the following arbitrary scale of 'constancy equivalents' is used:

	Species characteristic of Level (Table 1)	Species characteristic of 'mowing-marshes' (Lambert, 1946, pp. 260–1)
'Prominent species'	With constancy of 30% or over in one or more columns	With constancy of 3 or over in one or more columns
'Inconspicuous species'	With constancy below 30% in all columns, but not less than 10% in at least one column	With constancy less than 3 in all columns, but reaching 2 in at least one column
'Very inconspicuous species'	Present in region, but constancy not reaching 10% in any column	Present in region, but constancy not reaching 2 in any column

It should be noted that the use of the terms 'prominent' and 'inconspicuous', though employed here for convenience, is based only on constancy data, without reference to relative frequencies. Nevertheless, even with the limitations mentioned, the comparison of the two lists showed certain features of interest; the results are therefore incorporated in Tables 2 and 3, which include all species which are 'prominent' in at least one of the two regions.

In these two tables, the species are compared in relation to the two major modifying factors of grazing intensity and soil differences. Since the effect of differences in drainage conditions between the 'mowing-marshes' and the Level was thought to operate mainly in relation to renewal of mineral supply in the former, it is therefore indirectly incorporated in Table 3; general observation showed that its differential effect on the height of the water-table in relation to the surface in the two regions had a less significant effect on the general distribution of the vegetation than the other two factors, but a detailed consideration of this must await further evidence.

In Table 2, a comparison of the first two columns will show that a large number of species which are prominent on the 'mowing-marshes' are absent or play only an inconspicuous part in the Level; of the latter, only a very few are able to persist under relatively heavy grazing without some diminution in constancy. The proportion of species characteristic of the true 'mowing-marshes' is naturally greater in those areas of the Level which are now neglected and rarely mown, or only lightly grazed, but since even here grazing has only been relaxed fairly recently many 'mowing-marsh' species have not yet gained entry or become abundant.

Table 2. *Comparison of species on 'mowing-marshes' and on Level in relation to biotic factors*

Species prominent on 'mowing-marshes' but absent or very inconspicuous on Level	Species prominent on 'mowing-marshes' but relatively inconspicuous on Level	Species prominent both on 'mowing-marshes' and on Level	Species prominent on Level but relatively inconspicuous on 'mowing-marshes'	Species prominent on Level but absent or very inconspicuous on 'mowing-marshes'
SPECIES PREDOMINANT IN MOWN OR NEGLECTED AREAS				
Caltha palustris		*Species present only in mown areas*		
Calystegis sepium	Eupatorium cannabinum			
Carex appropinquata				
C. elata				
C. paniculata			*Species persisting only under very light grazing*	
C. riparia				
Epilobium hirsutum				
E. parviflorum				
Lychnis flos-cuculi	Angelica sylvestris	Galium uliginosum		
Myosotis palustris	Iris pseudacorus			
Peucedanum palustre	Lysimachia vulgaris			
Polygonum amphibium f. terrestre	Thalictrum flavum			
Rumex hydrolapathum		*Species persisting but generally diminishing under heavy grazing*		
Scabiosa succisa				
Sium erectum				
Solanum dulcamara				
Stachys palustris	Festuca elatior	Lotus uliginosus	Hydrocotyle vulgaris	
Urtica dioica	Lythrum salicaria	Molinia caerulea		
Valeriana dioica	Vicia cracca	Phragmites communis		
V. officinalis				
SPECIES SHOWING NO MARKED DIFFERENCE IN CONSTANCY BETWEEN MOWN AND GRAZED AREAS				
	Galium palustre	Glyceria maxima	Plantago lanceolata	Carex flacca
	Phalaris arundinacea			
	Ranunculus acris			
SPECIES FAVOURED BY LIGHT GRAZING, BUT DIMINISHING UNDER HEAVY GRAZING				
	Cirsium palustre	Filipendula ulmaria		Alopecurus geniculatus
		Juncus subnodulosus		Poa trivialis
		Ranunculus repens		
SPECIES FAVOURED BY INCREASING INTENSITY OF GRAZING				
	Carex acutiformis	Holcus lanatus	Agrostis stolonifera	Festuca rubra
	Equisetum palustre		Potentilla anserina	Juncus effusus var. compactus

The centre column of Table 2 shows that a few species are fairly characteristic of both regions, though even of these the greater proportion diminish under heavy grazing. In this column are included the three species already discussed in more detail—i.e. *Phragmites communis* (predominant in mown or neglected areas), *Glyceria maxima* (showing no marked difference in constancy between the mown and grazed areas), and *Juncus subnodulosus* (favoured by light grazing but diminishing where this is heaviest).

With the exception of the low-growing *Hydrocotyle vulgaris*, which is less constant though persisting under heavy grazing, those species which are more characteristic of the Level than of the 'mowing-marshes' (columns 4 and 5 of Table 2) are all resistant to a considerable amount of grazing, and the majority are favoured by it. Species in this category include the smaller pasture grasses (such as *Agrostis stolonifera*, *Alopecurus geniculatus* and *Festuca rubra*), rosette and creeping forms (such as *Plantago lanceolata* and *Potentilla anserina*), and taller forms avoided by stock (such as *Juncus effusus* var. *compactus*).

In Table 3, an attempt is made to compare the vegetation of the Level with that of the 'mowing-marshes' in respect of edaphic factors. A direct comparison here is somewhat complicated by the different basis of grouping of the species in the lists from the two regions. In the original 'mowing-marsh' list, the subsidiary species were grouped as they occurred in relation to the three main dominants, i.e. *Glyceria maxima*, *Phragmites communis* and *Juncus subnodulosus*; but in Table 1 of the present paper the species of the Level are classified in direct relation to the peat or clay substrate. Since, however, it has been shown that the relation between *Glyceria* and *Juncus* as dominants on the 'mowing-marshes' is itself determined predominantly by edaphic considerations, these two species may perhaps justifiably be regarded as indicators of substrate conditions as a whole. The predominance of *Glyceria* on the clay of the Level, and of *Juncus* on the peat, suggests that a direct comparison may be made between the other species occurring on the clay with those of the 'mowing-marsh' Glycerietum, while those of the peat may be compared with those of the 'mowing-marsh' Juncetum.

If this basis for comparison is used, it may be seen from Table 3 that a very close correlation exists between the vegetation of the two regions with respect to edaphic conditions. The only significant discrepancies occur in the case of *Phragmites communis* (predominant towards the Glycerietum of the 'mowing-marshes' but on the peat of the Level) and of *Holcus lanatus*, *Agrostis stolonifera* and *Potentilla anserina* (all more characteristic of the Juncetum of the 'mowing-marshes' but predominant on clay in the Level). As regards *Phragmites*, which appears tolerant of a fairly wide range of edaphic conditions, the discrepancy is negligible when the actual constancy numbers themselves are considered, since the bias towards one set of conditions or the other is very slight in either region. The main interest lies in a consideration of the other three. These are all low-growing species, unable to compete with the tall vigorous *Glyceria* of the 'mowing-marshes' and consequently excluded there from soils which suit them best, though able to exist as relatively insignificant subsidiary species on the less favourable substrates occupied by the shorter *Juncus*; but on the Level, where the growth of *Glyceria* is kept in check by grazing, they are able to predominate within the clay areas. The other pasture grasses (i.e. *Alopecurus geniculatus*, *Festuca rubra* and *Poa trivialis*) which are very inconspicuous or absent on the 'mowing-marshes', are likewise predominant on the clay of the Level, where they are accompanied in some areas by *Lolium perenne* and in wetter parts by *Glyceria fluitans* (both insufficiently constant to warrant inclusion in Tables 2 and 3).

Table 3. *Comparison of species on 'mowing-marshes' and on Level in relation to edaphic factors*

SPECIES OCCURRING PREDOMINANTLY IN GLYCERIETUM OF 'MOWING-MARSHES' OR ON CLAY IN LEVEL

Species prominent on 'mowing-marshes' but absent or very inconspicuous on Level		Species prominent on 'mowing-marshes' but relatively inconspicuous on Level		Species prominent both on 'mowing-marshes' and on Level		Species prominent on Level but relatively inconspicuous on 'mowing-marshes'		Species prominent on Level but absent or very inconspicuous on 'mowing-marshes'
In Glycerietum of 'mowing-marshes'	On clay in Level	In Glycerietum of 'mowing-marshes'	On clay in Level	In Glycerietum of 'mowing-marshes'	On clay in Level	In Glycerietum of 'mowing-marshes'	On clay in Level	On clay in Level
Caltha palustris Calystegia sepium Carex riparia Epilobium hirsutum Myosotis palustris Peucedanum palustre Rumex hydrolapathum Solanum dulcamara Stachys palustris Urtica dioica		Equisetum palustre Phalaris arundinacea	Carex acutiformis Lysimachia vulgaris	Glyceria maxima Phragmites communis	Holcus lanatus		Agrostis stolonifera Potentilla anserina	Alopecurus geniculatus Festuca rubra var. Juncus effusus compactus Poa trivialis

SPECIES SHOWING NO MARKED DIFFERENCE IN CONSTANCY BETWEEN GLYCERIETUM AND JUNCETUM OF 'MOWING-MARSHES' OR BETWEEN CLAY AND PEAT OF LEVEL

Species prominent on 'mowing-marshes' but absent or very inconspicuous on Level		Species prominent on 'mowing-marshes' but relatively inconspicuous on Level		Species prominent both on 'mowing-marshes' and on Level		Species prominent on Level but relatively inconspicuous on 'mowing-marshes'		Species prominent on Level but absent or very inconspicuous on 'mowing-marshes'
In 'mowing-marshes'	On Level	In 'mowing-marshes'	On Level	In 'mowing-marshes'	On Level	In 'mowing-marshes'	On Level	On Level
Carex paniculata Valeriana officinalis		Angelica sylvestris Lythrum salicaria	Carex acutiformis Lysimachia vulgaris Cirsium palustre					•

SPECIES OCCURRING PREDOMINANTLY IN JUNCETUM OF 'MOWING-MARSHES' OR ON PEAT IN LEVEL

Species prominent on 'mowing-marshes' but absent or very inconspicuous on Level		Species prominent on 'mowing-marshes' but relatively inconspicuous on Level		Species prominent both on 'mowing-marshes' and on Level		Species prominent on Level but relatively inconspicuous on 'mowing-marshes'		Species prominent on Level but absent or very inconspicuous on 'mowing-marshes'
In Juncetum of 'mowing-marshes'	On peat in Level	In Juncetum of 'mowing-marshes'	On peat in Level	In Juncetum of 'mowing-marshes'	On peat in Level	In Juncetum of 'mowing-marshes'	On peat in Level	On peat in Level
Carex appropinquata C. elata Epilobium parviflorum Lychnis flos-cuculi Polygonum amphibium f. terrestra Scabiosa succisa Sium erectum Valeriana dioica		Festuca elatior Galium palustre Iris pseudacorus Ranunculus acris Thalictrum flavum Vicia cracca	Cirsium palustre	Filipendula ulmaria Galium uliginosum Juncus subnodulosus Lotus uliginosus Molinia caerulea Ranunculus repens Holcus lanatus	Phragmites communis		Hydrocotyle vulgaris Plantago lanceolata Agrostis stolonifera Potentilla anserina	Carex flacca

Although the smaller grasses as a group occur more typically on the clay of the Level than on the peat, they are by no means entirely excluded from the latter, and some, such as *Holcus lanatus* and to a less extent *Festuca rubra*, are relatively abundant on the more heavily grazed parts; nevertheless, there is a tendency for them to be replaced on the peat by *Carex flacca*, which appears equally resistant to heavy grazing, and which forms a dense mat over the ground in many places.

D. DISCUSSION

At first sight it must appear that the vegetation of the Level as a whole is governed by a very different complex of ecological factors from that of the 'mowing-marshes'. Not only has the biotic factor of grazing a far more modifying effect on the vegetation than that of mowing, but in addition the drainage system is of an entirely different type, with embankment of the area excluding altogether the influx of mineral-rich water from the tidal river. But although differences in the general character of the vegetation were no doubt very marked in the past, the increasing difficulty of adequate drainage, with its accompanying relaxation of grazing in many parts, has allowed the establishment and spread of many species which are more characteristic of the 'mowing-marshes' than of grazed land. The balance existing between these 'mowing-marsh' species and the more typical pasture plants is naturally primarily dependent upon the present intensity of grazing in the various areas, and in this respect it is not always easy to distinguish clearly between cause and effect, since those areas bearing the best pasture plants tend to be the more heavily grazed and vice versa. This latter direct relationship is, however, to some extent nullified by differences in ownership, and hence in degree of exploitation, of separate though adjacent areas (cf. Fig. 2) and therefore affects the general interpretation of the vegetation less than might be assumed.

The differences between the drainage system of the Level and that of the 'mowing-marshes' appear to have had a less modifying influence on the present character of the vegetation than at first appeared to be the case. The inefficiency of the pumping system at the time of the survey, together with the general lowering of the surface through peat wastage, has until now allowed water-logged conditions through the greater part of the year similar to those of the 'mowing-marshes', so that both regions resemble each other in the general height of their water-tables. The exclusion of mineral-rich tidal water is a more serious factor, and it is therefore not surprising that the 'mowing-marsh' species which occur in the peat areas of the Level are those which are least dependent on the influence of tidal water (i.e. those of the Juncetum) in the 'mowing-marshes' themselves. But the presence of the clay substrate over a large part of the Level appears to some extent to compensate for the absence of flooding river water, and the clay areas are therefore able to bear species which in the 'mowing-marshes' are most characteristic of areas accessible to tidal water (i.e. those of the Glycerietum).

The clay tongue running up the valley naturally affects the vegetation most in those regions where it is exposed by wastage of the surface peat through drainage. In the unembanked 'mowing-marshes' between Rockland and Surlingham Broads (see Fig. 1), it is covered by almost a metre of peat so that its direct effect on the vegetation there is probably negligible. According to Pallis's original map (Fig. 3), the clay peters out some distance below Surlingham Broad, roughly in the region of Coldham Hall; but an isolated

boring by J. N. Jennings (1947, unpublished), made well beyond the bend of the river and further upstream than the largest remaining open water area of Surlingham Broad, has established the extension of the clay past this point. The clay, therefore, undoubtedly underlies part of the two derelict embanked areas in the vicinity of Surlingham Broad (see Fig. 1), and although its lateral limits have not yet been traced, it has been found there very near the surface in one of two exploratory soil pits. Although these two areas are now completely water-logged and derelict, and peat is again forming within them, the thickness of the original surface peat must have been so much reduced by earlier drainage that where the clay occurs the present surface level is still only a little above it. Hence the presence of the clay may be expected to have the same effect on the vegetation of these embanked areas as has been shown for the Rockland-Claxton Level, and with this assumption the hitherto puzzling occurrence of several apparent anomalies in the distribution of species in these areas may be explained.

Although it is outside the scope of this paper to deal with these two derelict embanked areas in detail, it can now be seen that their present vegetation represents an interesting transitional type between that of the embanked and still partially grazed Rockland-Claxton Level, and that of the unembanked 'mowing-marshes'. Parts of these areas now have renewed access of tidal water due to the disrepair of sluices and banks (together with the removal of the original oil pump from the upper area in 1914), so that their vegetation is now in essentials like that of the unembanked and rarely cut 'mowing-marshes'. In contrast, other parts are still removed from tidal influence, though they have been completely unexploited for several years, so that their vegetation approximates to that of the neglected areas of the Rockland-Claxton Level. And finally, in all parts there are local variations in constituent species which cannot be entirely ascribed to differences in access or otherwise of tidal water, but which may be satisfactorily explained by the assumption of a continuous clay substrate, just below the surface of the re-forming peat, on their riverward side.

E. SUMMARY

1. The Rockland-Claxton Level is an embanked and drained grazing area situated in the Yare valley, immediately south of Rockland Broad. It has undergone considerable degradation within the last 35 years owing to increased difficulty of drainage, with the result that it now bears many species more characteristic of the adjacent 'mowing-marshes' than of grazing land.

2. Grazing intensity varies considerably over the Level, and an attempt is made to correlate the present vegetation with this factor.

3. The Level is situated partly upon deep peat and partly upon clay, the latter having been deposited by a previous marine transgression of the valley and subsequently exposed by wastage of the surface peat above it; the distribution of species in relation to this is also considered.

4. A detailed comparison of the vegetation of the Level with that of the adjacent 'mowing-marshes' shows that the presence of the clay has approximately the same effect as the access of non-brackish tidal water on the relative distribution of species which are common to both regions.

5. Two other embanked areas, previously drained and grazed but now completely derelict, occur within the Surlingham-Rockland peat basin; the vegetation of these

appears to be transitional between that of the Rockland-Claxton Level and that of the true 'mowing-marshes', with an underlying extension of the clay exerting a similar effect as in the Level itself.

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THE FLORA OF CAMBRIDGE WALLS

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(*With Plates* 18 *and* 19 *and one Figure in the Text*)

CONTENTS

1. INTRODUCTION

This paper gives an account of observations made in and around Cambridge during the years 1937–40, and at intervals since then. Interest was first stimulated by the great variety of plants growing on walls in the town itself, although growth is seldom as luxuriant as it is on walls in parts of the country with a higher rainfall. The aim of the work has been to analyse the composition, life-form and dispersal mechanism of the plants. Factors influencing colonization and growth were investigated, and attention was particularly directed to some striking effects of aspect and shading. Some examples of succession on walls were also studied.

It must be admitted at the outset that time has not allowed more than an approach to the subject. A considerably longer period of observation would be desirable for the study of successional changes, for example. Detailed analysis of the substratum was difficult, since there were limitations to the collection of samples. Representative lists were compiled in a number of villages and in the city of Ely, as well as in Cambridge, but all records were made within the county of Cambridgeshire. Only those plants which appeared to be naturally established have been recorded; the great majority are from walls, but a few interesting records from other buildings and bridges have been included.

2. THE FLORA OF WALLS

(a) Composition

In Cambridge itself, old college walls provide many habitats suitable for plants and it is probably this factor, combined with the comparative freedom of the town from smoke, which has allowed the establishment of so many species. The list given in Table 1, although not complete, is believed to be representative.

It is not easy to separate all these plants into definite groups, for many are found in a wide variety of habitats. Certain groups are, however, reasonably distinct. In Table 2

Table 1. *List of Cambridge wall plants.*

Angiosperms

Acer pseudo-platanus L.
Achillea millefolium L.
Acinos arvensis (Lam.) Dandy n.comb.
Aesculus hippo-castanum L.
Agropyron repens (L.) Beauv.
Agrostis stolonifera L.
Alnus glutinosa (L.) Gaertn.
Alopecurus myosuroides Huds.
Angelica sylvestris L.
Anthriscus sylvestris (L.) Hoffm.
Antirrhinum majus L.
Apium nodiflorum (L.) Lag.
Arabis hirsuta Br.
A. turrita (L.) Scop.
Arenaria leptoclados (Rchb.) Guss.
A. serpyllifolia L.
Arrhenatherum elatius (L.) J. & C. Presl.
Asparagus officinalis L.
Atriplex hastata L.
Ballota nigra L.
Barbarea vulgaris (R.) Br.
Bellis perennis L.
Betula pendula Roth.
Brachypodium sylvaticum (Huds.) Beauv.
Bromus sterilis L.
Bryonia dioica Jacq.
Buddleja davidii Franch.
Calystegia sepium (L.) R. Br.
Campanula rapunculoides L.
Capsella bursa-pastoris (L.) Medic.
Cardamine hirsuta L.
C. pratensis L.
Carex riparia Curt.
C. vulpina L.
Centranthus ruber (L.) DC.
Cerastium semidecandrum L.
C. viscosum L.
C. vulgatum L.
Chamaenerion angustifolium (L.) Scop.
Cheiranthus cheiri L.
Chelidonium majus L.
Chrysanthemum parthenium (L.) Bernh.
Cirsium arvense (L.) Scop.
C. vulgare (Savi) Ten.
Convallaria majalis L.
Convolvulus arvensis L.
Corydalis lutea (L.) DC.
Corylus avellana L.
Cotoneaster horizontalis Decn.
Crataegus monogyna Jacq.
Crepis capillaris (L.) Wallr.
C. taraxacifolia Thuill.
Dactylis glomerata L.
Descampsia caespitosa (L.) Beauv.
Diplotaxis muralis (L.) DC.
Epilobium hirsutum L.
E. montanum L.
E. parviflorum Schreb.
E. roseum Schreb.
E. tetragonum L.
Erigeron canadensis L.
Erinus alpinus L.
Erophila verna (L.) Chevall.
Euphorbia peplus L.
Festuca gigantea (L.) Vill.
F. ovina L.
F. rubra L.

Filipendula ulmaria (L.) Maxim.
Fraxinus excelsior L.
Galium anglicum Huds.
G. aparine L.
G. palustre L.
Geranium robertianum L.
Geum urbanum L.
Glechoma hederacea L.
Hedera helix L.
Helxine soleirolii Req.
Heracleum sphondylium L.
Hieracium pilosella L.
Holcus lanatus L.
Holodiscus discolor Maxim.
Hordeum murinum L.
Hypericum perforatum L.
Hypochoeris radicata L.
Jasminum nudiflorum Lindb.
Juncus articulatus L.
Koeleria gracilis Pers.
Laburnum anagyroides Medic.
Lactuca serriola L.
Lamium album L.
L. maculatum L.
L. purpureum L.
Lapsana communis L.
Leontodon hispidus L.
Linaria cymbalaria (L.) Mill.
L. purpurea (L.) Mill.
Lolium perenne L.
Lychnis alba Mill.
Lycium halamifolium Mill.
Lycopus europaeus L.
Mahonia aquifolium (Pursh.) Nutt.
Matricaria chamomilla L.
M. matricarioides (Less.) Porter
Medicago lupulina L.
Mentha aquatica L.
Myosotis arvensis (L.) Hill
Nasturtium officinale (R.) Br.
Papaver atlanticum (Ball.) Cosson.
P. rhoeas L.
Parietaria diffusa Mert. & Koch.
Philadelphus pallidus Hayek.
Phleum pratense L.
Plantago lanceolata L.
P. major L.
P. media L.
Platanus sp.
Poa annua L.
P. compressa L.
P. nemoralis L.
P. pratensis L.
Polygonum aviculare L.
Potentilla anserina L.
P. reptans L.
Prunella vulgaris L.
Ranunculus bulbosus L.
R. repens L.
R. sceleratus L.
Reseda lutea L.
R. luteola L.
Ribes grossularia L.
R. rubrum L.
Rosa sp.
Rubus fruticosus agg.
Rumex acetosa L.
R. conglomeratus Murr.
R. crispus L.

Table 1 (*continued*)

Rumex hydrolapathum Huds.
R. sanguineus L.
Ruscus aculeatus L.
Sagina apetala Ard.
S. procumbens L.
Salix alba L.
S. atrocinerea Brot.
Sambucus nigra L.
Saxifraga tridactylites L.
Scleropoa rigida (L.) Griseb.
Scrophularia aquatica L.
Scutellaria galericulata L.
Sedum acre L.
S. album L.
Sempervivum tectorum L.
Senecio jacobea L.
S. viscosus L.
S. vulgaris L.
Sinapis arvensis L.
Sisymbrium officinale (L.) Scop.
Solanum dulcamara L.
S. nigrum L.
Solidago canadensis L.
Sonchus arvensis L.
S. asper (L.) Hill.
S. oleraceus L.
Sorbus aucuparia L.
Stellaria media (L.) Vill.
Syringa vulgaris L.
Taraxacum officinale Weber.
Trifolium campestre Schreb.
Trisetum flavescens (L.) Beauv.
Triticum sp.
Tussilago farfara L.
Ulmus sp.
Urtica dioica L.
Verbascum thapsus L.
Veronica arvensis L.
V. beccabunga L.
V. hederaefolia L.
V. polita Fr.
Viola riviniana Rchb.

Gymnosperms
Taxus baccata L.

Pteridophytes
Asplenium adiantum-nigrum L.
A. ruta-muraria L.
A. trichomanes L.
Dryopteris filix-mas agg.
Phyllitis scolopendrium (L.) Newm.

Polypodium vulgare L.
Pteridium aquilinum (L.) Kuhn.

Bryophytes
Amblystegium filicinum De Not.
A. serpens B. & S.
Barbula convoluta Hedw.
B. revoluta Brid.
B. rigidula Mitt.
B. sinuosa Braithw.
B. tophacea Mitt.
B. vinealis Brid.
Brachythecium albicans B. & S.
B. rutabulum B. & S.
Bryum argenteum L.
B. caespiticium L.
B. capillare L.
Bryum sp.
Camptothecium sericeum Kindb.
Ceratodon purpureus Brid.
Eurhynchium confertum Milde.
E. rusciforme Milde.
Fontinalis antipyretica L.
Funaria sp.
Grimmia apocarpa Hedw.
G. pulvinata Smith.
Hypnum cupressiforme L.
Orthotrichum anomalum v. *saxatile* Milde.
O. diaphanum Schrad.
Tortula intermedia Berk.
T. muralis Hedw.
T. ruralis Ehrh.
Webera carnea Schp.
Lophocolea bidentata (L.) Dum.
Lunularia cruciata (L.) Dum.
Marchantia polymorpha L.

Algae
Chlorococcum sp.
Cladophora glomerata (L.) Kütz.
Hormidium flaccidum (Kütz.) A. Br.
Oedogonium sp.
Prasiola crispa (Lightf.) Menegh.
Trentepohlia aurea Mart.

Totals

Angiosperms	178
Gymnosperms	1
Pteridophytes	7
Bryophytes	32
Algae	6

Table 2. *The number of plants recorded in various lists and also found on Cambridge walls*

Situation	Authority	Total	Common to Cambridge walls
			Number of species
(a) Vascular plants			
Walls in the Oxford district	Church (1922)	33	20
City wall, Canterbury	Author (partial list, unpublished)	22	22
Churches in Poitiers	Richard (1888)	˙76	43
Bombed sites in London	Salisbury (Fitter, 1945)	126	70
Pollard willows near Cambridge	Willis & Burkill (1893)	80	50
(b) Mosses			
Middlesex walls	Richards (1928)	14	10

the Cambridge wall list is compared with others made in a variety of situations and recorded in the literature. The list of plants from bombed sites has been included because of some similarity in the substratum and that from the pollard willows because similar problems of dispersal are involved. It is interesting to find that, in each instance, more than half the total number of species also grow upon Cambridge walls. This suggests that certain plants may be found fairly regularly in these situations. Several plants in the Cambridge list are in fact widely found on walls throughout Britain, typical examples being *Cheiranthus cheiri*, *Linaria cymbalaria*, *Parietaria diffusa*, *Poa compressa* and *Asplenium ruta-muraria*.

Garden escapes include a wide range extending from rock plants such as *Erinus alpinus* to ornamental shrubs and seedlings of large trees such as *Aesculus hippo-castanum*, and these account for the majority of the thirty-six species in the list which are not native to the country. The wall plants include some typical of dry situations such as *Sedum acre*, *Saxifraga tridactylites* and *Scleropoa rigida*, together with many others characteristic of waste ground, fields and hedgerows. Twenty-three species were recorded from the villages only, and several others such as *Sisymbrium officinale*, *Crepis capillaris* and *Poa pratensis* were more frequently found in the villages than in Ely and Cambridge. The riverside walls in Cambridge had a varied flora, including some twenty-four species characteristic of wet situations. These last, together with four mosses and *Marchantia polymorpha*, were confined to positions near water-level, whereas *Fontinalis antipyretica* was common on the submerged portions of walls.

Some species of wall plants have been found in their present localities for a very long time. Thus, in Cambridge, *Arabis turrita* was recorded by Prof. T. Martyn in 1763 and *Polypodium vulgare* by John Ray (Catalogus Cantabrigiam, 1660), the latter species in the position it still occupies. Many annuals also appear regularly on walls in places where they were recorded in the last century. Yet, in contrast with this, *Alopecurus myosuroides* was seen in 1939 but not afterwards. *Galium anglicum* is an interesting species which may formerly have been more widespread, but now appears to be confined to walls in Ely. *Helxine soleirolii* is an example of a recent arrival and has become established on moist stone-work in two localities.

Table 3. *The number of records of the commoner Cambridge wall plants*

Poa annua	83	*Sambucus nigra*	32
Taraxacum officinale	54	*Senecio vulgaris*	30
Festuca rubra	54	*Chrysanthemum parthenium*	29
Antirrhinum majus	47	*Acer pseudo-platanus*	25
Linaria cymbalaria	46	*Capsella bursa-pastoris*	25
Arenaria serpyllifolia	38	*Chamaenerion angustifolium*	24

Table 3 gives a list of the flowering plants more frequently found on the walls; it is perhaps noteworthy that two trees are included. *Sambucus nigra* seems able to establish itself in a remarkable variety of places; it may even colonize the inside of chimney pots.

(b) Life-form

Nearly half the Cambridge wall plants are hemicryptophytes. In exposed positions the plants may be dwarf, but more frequently they nearly attain their normal height. Flowering is regular, and very few species have been recorded as failing to flower. Therophytes account for over a quarter of the species. Diminutive forms, similar to those

described by Church (1922) on Oxford walls, are abundant on some exposed wall tops; they also resemble closely the annuals found on East Anglian grasslands. Therophytes commonly flower from April to mid or late May and then soon shrivel, although they may reappear in autumn. *Senecio vulgaris* and *Capsella bursa-pastoris*, for example, may flower sporadically until January in a mild winter.

15 % of the flowering plant species are phanerophytes. This high proportion is probably to be explained by the fact that many of the walls border gardens having a considerable variety of trees and shrubs, and that many walls are of considerable age. Phanerophytes are commonly present as seedlings, but well-developed young trees of *Acer pseudo-platanus* (up to 1·2 m.), *Sorbus aucuparia* and *Betula pendula* (up to 1·8 m.) are sometimes to be seen. The root systems of two such trees were found to be much distorted. The main root of one (*Sambucus nigra*) followed an irregular course towards the ground, growing between

Table 4. *Comparison of species lists with regard to life-form and dispersal*

	Cambridge walls				London bomb-sites				Poitiers churches		Cambridge pollard willows			
	Species		Site records		Species		Site records		Species		Species		Site records	
	No.	%	No.	%	No.	%	No.	%	No.	%	No.	%	No.	%
					(a) Life-form									
Phanerophytes	24	15	157	13	7	5	21	2	4	5	18	22	1791	52
Chamaephytes	7	4	66	5	3	2	7	1	3	4	2	3	23	1
Hemicryptophytes	79	49	603	48	55	44	357	37	37	49	49	61	879	25
Geophytes	8	5	42	3	7	5	76	8	2	3	2	3	1	—
Therophytes	44	27	389	31	54	44	505	52	30	39	9	11	746	22
					(b) Dispersal									
By animals:														
Fleshy	20	13	89	7	5	4	27	3	3	4	19	24	1763	45
Adhesive	5	3	44	4	3	2	14	1	—	—	4	5	957	24
By wind:														
Winged, etc.	79	50	564	45	45	36	723	75	32	42	33	41	995	25
Not modified	58	34	560	44	73	58	202	21	41	54	24	30	236	6
Totals	162		1257		126		966		76		80		{3440* {3951	

* The lower total for life-form is caused by the exclusion of unidentified grasses.

the bricks at some places horizontally and at others vertically. The other (*Sorbus aucuparia*) grew on a wall having at the top a layer of rounded bricks, under which the main roots were situated. These extended more than a metre in each direction along the wall and sent fan-like branches of fine roots upwards between the bricks.

Comparison with three of the published lists already mentioned (p. 138) is shown in Table 4. Riparial species have been excluded from the Cambridge wall list for this purpose. For the two Cambridge lists, the unit 'site record' is the observation of the presence of a given species at a given site such as a length of wall or a pollard willow top, at any time during the period of observation (in the case of the Cambridge walls, a discontinuous period of 10 years). It has no reference to the frequency of individual plants on the site. The London list shows the percentage of bombed sites in which a given plant has been recorded, figures for percentage occurrence being available for just under half the total number of species listed. Detailed figures are not available for the Poitiers churches. Although these records were made in somewhat different ways, they show certain interesting features.

The proportion of life-forms in the case of Cambridge wall plants is similar to that of the bombed sites both in respect of species and site records, but there are more phanerophytes and less therophytes. This probably reflects the early stage of colonization of the bombed sites. Species present on the Poitiers churches have a distribution of life-form very similar to those of the London bombed sites. Here, exposure and lack of suitable places for establishment may have restricted the growth of phanerophytes. By contrast with the conditions present on the Cambridge walls and Poitiers churches, the accumulation of humus and the relatively sheltered habitat provided by the tops of the pollard willows might be expected to favour the establishment of phanerophytes. The relatively high proportion of these plants present on pollard willows is evident from the site records. Here dispersal is also an important factor, and will be considered in the next section.

(c) Dispersal

The methods of dispersal of the plants in the four lists are also compared in Table 4. Cambridge walls have a high proportion of wind-distributed plants many of which have no definite wind-dispersal mechanism although the seeds are small. This tendency in wall plants has already been noted by Ridley (1930). The bombed sites of London and the Poitiers churches have an even higher proportion of wind-distributed plants. The fact that 75% of the records from bombed sites are of plants having a definite modification assisting dispersal by wind further emphasizes the early stage of colonization of these open situations. Dispersal by birds is more frequent on Cambridge walls than in London and Poitiers, probably because the walls are often close to garden trees and shrubs and hence frequently visited by birds. Birds play an even greater part in dispersal on pollard willows, and nest building was shown by Willis & Burkill (1893) to be important in this respect. The importance of short-distance dispersal, which is apparent from the description of the pollard willow flora in different districts, is also evident in the case of walls (p. 145). Seventeen of the twenty-four species confined to river walls in Cambridge are well known to be dispersed by water, and it is likely that most of the other plants growing near water-level were established from seed blown into the river and then washed into crevices.

3. Factors influencing colonization and growth

The numerous factors controlling the composition of wall vegetation include those connected with the structure of the wall and those due to its function and position; they are to a considerable extent interrelated.

(a) Materials of construction

The materials of which walls are made influence the rate of weathering and hence determine in part the opportunities for colonization by plants. Concrete walls normally have few cracks and seldom bear flowering plants. Brick walls, on the other hand, soon develop small cracks, especially where the mortar is of poor quality, and therefore frequently bear flowering plants.

In the Cambridge district, materials used in wall construction provide a substratum of circum-neutral or alkaline reaction. Samples of such material and of the humus accumulated by mosses were found to have a pH range of 6·4–8·4. Oxyphilous plants therefore tend to be excluded.

(b) Moisture

The extent to which a wall retains moisture depends on the materials of which it is made, its situation, and its function. In this connexion, little is known of the effect of materials but it is clear that a supporting wall, with earth banked up on one side, will tend to hold moisture to a greater extent than a free wall. The effect of a supply of surface moisture on wall vegetation is particularly striking. Intermittent overflows from gutters or pipes often allow the establishment of a variety of plants, including ferns, on the vertical sides of walls, which are otherwise bare. In such instances the increased weathering caused by the flow of water presumably assists this establishment. Growth of higher plants upon relatively unweathered walls is limited to horizontal or sloping surfaces, and slope also controls the distribution of mosses to a certain extent. This is almost certainly connected with the supply of moisture from rain, for commonly most of the water running off wall tops is absorbed by the bricks before it has flowed more than about 0·5 m.

For this reason, a free wall receiving moisture from rainfall alone commonly shows a zonation of plants: the top may bear mosses such as *Tortula muralis* and *Grimmia pulvinata* and also a few flowering plants. The vertical sides may have moss growth confined to the first 30 cm. or so at the top and to about 10 cm. at the base. In this latter position, mosses such as *Barbula vinealis* and *Bryum argenteum* are frequently found, and *Lunularia cruciata* may also be present. More continuous moss growth may be found on vertical walls under different conditions. One interesting example of the effect of aspect was seen on an old brick wall in the village of Grantchester. The west side had a more or less uniform moss cover, with lichens slightly more abundant at the base (Pl. 18, phot. 1). This side was found to be almost uniformly damp after a heavy shower of rain. The east side had a zone of moss towards the top, one of lichen in the middle, and was bare below (Pl. 18, phot. 2); after the same shower, it had irregular damp patches towards the top but was dry at the base. On a recently rebuilt section of this same wall, water flowing off the top was after a short distance confined to certain courses; this effect was probably associated with differences in the porosity of the brick. Here, on an otherwise bare surface, moss was colonizing the centre of such a course and lichen the edges (Pl. 18, phot. 3). A study of older walls suggested that the position of moss colonies on the vertical sides was determined to some extent by this tendency for run-off water to follow certain courses.

A special instance of the influence of moisture is provided by the riverside walls, which are in addition supporting walls for a part or the whole of their height. The water-level of the River Cam seldom fluctuates on them more than 30–40 cm. during the year and would not therefore be expected greatly to affect the distribution of plants. It was, in fact, noted that wall plants developed normally in the season following the floods of March 1947, when the river rose just over 1 m. above summer level for several days. The majority of riparial species such as *Lycopus europaeus*, *Mentha aquatica* and *Ranunculus sceleratus* tend to occupy positions 10–15 cm. above the normal summer level of the river. In some places a fairly well-marked zonation of lower plants is found; thus in one situation the following were recorded:
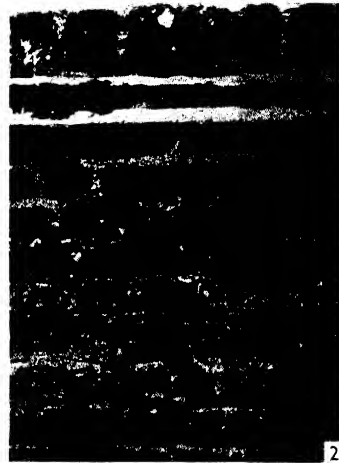
River level	River level–20 cm.	20–60 cm.
Cladophora glomerata	*Cladophora glomerata*	*Tortula muralis*
Oedogonium sp.	*Bryum* sp.	*Barbula convoluta*
	Amblystegium filicinum	*Amblystegium filicinum*
	Barbula tophacea	
	Lunularia cruciata	

Phot. 1. The west side of a brick wall with a moderately uniform cover of *Tortula muralis*. Lichens are more abundant towards the base.

Phot. 2. The east side of the same wall with an upper zone of mosses, mainly *Grimmia pulvinata* and *Barbula rinealis*, a middle zone of lichens, and a bare lower zone.
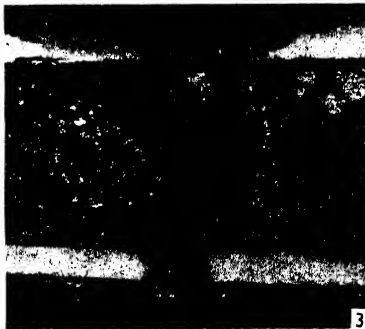

Phot. 3. A damp patch on a recently built brick wall, caused by water running off the top during a rain shower. Moss is colonizing the centre of the patch and lichen the edges.

Phot. 4. A contrast between the repointed section of a brick wall top, with colonies of *Tortula muralis* and *Grimmia pulvinata* and the original top, with a nearly continuous mat of *Camptothecium sericeum*.

Phot. 5. Seedlings of *Arenaria serpylli-folia* and *Poa annua* established in a mat of *Camptothecium sericeum* on the ledge of a brick wall.

Ledge
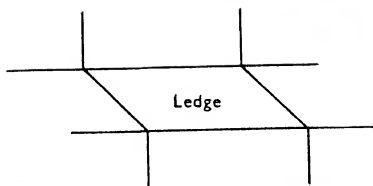
Phot. 6. A stage in the overgrowth of the mosses *Tortula muralis* and *Barbula vinealis* by a lichen. *Sedum album* is growing down from the wall top.

Even on these riverside walls, moisture from other sources allows many additional flowering plants to become established. In one instance, eight species were seen below an overflow pipe on an otherwise bare wall.

(c) Shade

Shade is important in determining the time during which a wall remains moist after rain. In extreme instances, plants growing on a stone surface facing south are exposed to considerable periods of drought and to wide fluctuations of temperature. Between this condition and one in which no direct sunlight is received all intermediates are found. An interesting example of the effect of aspect was found on the stone ledges of college bridges at Cambridge, those at Clare College, for example, having a flora as follows:

South aspect		North aspect	
Cerastium vulgatum		Cerastium vulgatum	
Festuca rubra		Linaria cymbalaria	
Linaria cymbalaria		Poa annua	
Poa annua		Sagina apetala	
Grimmia pulvinata	2	Camptothecium sericeum	5
Tortula intermedia	2	Tortula muralis	2
Barbula vinealis	1	Barbula rigidula	2
Tortula muralis	1	B. revoluta⎱ B. vinealis⎰	1

Numbers given for mosses here and in the following account refer to percentage cover as follows:
+, under 1   1, 1–5   2, 6–25   3, 26–50   4, 51–75   5, 76–100

The mosses formed isolated colonies on the south ledge but a nearly continuous mat on the north. On Trinity College bridge, growth of flowering plants was limited to a few individuals of *Poa annua*, whereas the moss cover showed a contrast between north and south ledges very similar to that described for Clare. *Hypnum cupressiforme* and *Brachythecium rutabulum* were also present on the northern side, however. St John's College bridge had a considerable growth of *Festuca rubra* on the south ledge only, as at Clare, but the mosses showed less contrast, probably as a result of partial shading by large trees on the south side. The distribution of flowering plants on St John's College bridge is shown in Fig. 1.
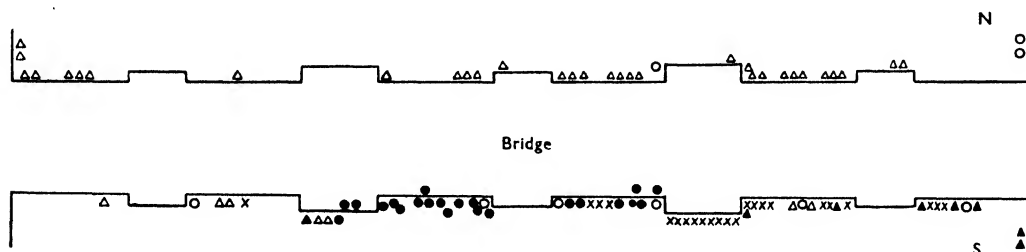

Fig. 1. The flowering plants on the stone ledges of St John's College Bridge.
Key: *Festuca rubra* ●, *Poa annua* △, *Sagina apetala* ×, *Senecio vulgaris* ▲, *Taraxacum officinale* ○

It was not easy to find a wall with different aspects for each of which the surface was comparable. A brick wall at the top of Castle Hill, Cambridge, provided reasonably satisfactory comparisons on a sloping ledge about 2·5 m. from the ground. The different sections of this wall provided a series of sites having an increasing exposure to sunlight. Thus, in early May, the north-east side received little sun after 11 a.m. and was completely shaded from noon onwards. The north-west had two sections, the first of which (*a*) received

no sun until about 2 p.m., being shaded by a high extension of the wall, whereas the second (*b*) was not shaded in this way and received sun from 10.30 a.m. onwards. The south-west side received sunlight earlier still. Table 5 records the moss cover and abundance of flowering plants on these sections. There is a big drop in the percentage cover of mosses on the south-west side, whereas the number of flowering plants is greater. A complex of factors is probably operative here: the degree of exposure to sunlight and perhaps also to wind may control the rate of drying of the wall, which would affect the growth of plants.

Table 5. *Estimates of the dominance and abundance of plants on different aspects of a wall*

	North-east	North-west (a)	North-west (b)	South-west
(a) Dominance of mosses				
(1) Cover of individual species*:				
Barbula vinealis	4	4	3	+
Bryum caespiticium	3	2	2	.
Tortula muralis	2	2	2	1
Bryum argenteum	+	+	.	+
Camptothecium sericeum	.	.	+	+
Tortula muralis	.	.	.	+
(2) Total percentage cover	80	70	60	5
(b) Abundance of flowering plants†				
Festuca rubra	1	1	3	3
Arenaria serpyllifolia	1	3	2	2
Antirrhinum majus	.	1	3	3
Sedum acre	.	.	3	1

* Cover expressed by units, as on p. 143.

† Abundance is based on the number of plants present per unit length of wall, and expressed by an arbitrary scale 1–5.

Similar differences were often seen on different sides of a single wall. Thus, on the sloping stone top of an exposed country wall the moss cover was as follows:

North side		South side	
Grimmia pulvinata	4	Grimmia pulvinata	1
G. apocarpa	1	G. apocarpa	+
Tortula muralis	1		
T. ruralis	+		

Similarly, the rounded top of another country wall, made of brick, had the following moss cover:

North-west side		South-east side	
Camptothecium sericeum	4	Grimmia pulvinata	1
Hypnum cupressiforme	2	Tortula muralis	+
Tortula muralis	1		

If the number of positions where a given plant grows on shaded and unshaded walls is recorded and the total number of possible positions is known, the 'shade' and 'sun' frequencies can be calculated. The ratio between these frequencies gives an approximate measure of the preference of a plant for particular situations. Table 6 gives some of these ratios, which illustrate the dependence on shade of several ferns and mosses.

(d) Situation

Lists of vascular plants from walls in four different situations are given in Table 7. Although variations of aspect and shading partly contributed to the differences, the type of situation clearly influenced the wall flora. Most of the plants in the first list were common on walls in the centre of Cambridge, although these walls often had fewer species than the example given. The wall in the residential area had only one species common to the previous list and the composition of the flora was influenced by the nearness of

Table 6. *The ratios of 'shade' to 'sun' frequency of some wall plants*

Species preferring sunny situations		Widely tolerant species		Species preferring shade	
		(a) Vascular plants			
Sedum acre	0·0	Poa annua	0·9	Acer pseudo-platanus	2·3
Cheiranthus cheiri	0·0	Taraxacum officinale	1·0	Asplenium ruta-muraria	4·1
Antirrhinum majus	0·2	Linaria cymbalaria	1·1	Pteridium aquilinum	8·1
Senecio vulgaris	0·4	Chrysanthemum parthenium	1·1		
Festuca rubra	0·5	Chamaenerion angustifolium	1·2		
		(b) Mosses			
Grimmia pulvinata	0·5	Tortula muralis	1·0	Barbula revoluta	2·8
Tortula ruralis	0·6	Bryum caespiticium	1·2	Brachythecium rutabulum	∞
		Camptothecium sericeum	1·3	Hypnum cupressiforme	∞

Table 7. *Lists of vascular plants from walls in different situations*

Main road near town centre

Antirrhinum majus
Cheiranthus cheiri
Chrysanthemum parthenium
Festuca rubra
Linaria cymbalaria
Poa annua
Sedum acre
Senecio vulgaris

Road in residential area

Anthriscus sylvestris
Asplenium ruta-muraria
Bromus sterilis
Lamium album
Phyllitis scolopendrium
Poa annua
Ribes grossularia
Senecio jacobaea
Urtica dioica

College garden wall

Acer pseudo-platanus
Antirrhinum majus
Betula pendula
Buddleja davidii
Chamaenerion angustifolium
Philadelphus pallidus
Poa annua
Reseda luteola
Sagina procumbens
Sempervivum tectorum
Senecio vulgaris
Taraxacum officinale
Urtica dioica

Village churchyard wall

Achillea millefolium
Alopecurus myosuroides
Arrhenatherum elatius
Bromus sterilis
Dactylis glomerata
Festuca rubra
Koeleria gracilis
Lamium album
Matricaria chamomilla
Sedum acre

gardens and uncultivated ground. The college garden wall chiefly differed from the first one in having young trees and shrubs, all of which grew in the garden. The village church wall, on the other hand, had six species which were either confined to village walls or were more frequent there than in the towns. These examples bring out clearly the effect of short-distance dispersal on the flora of walls.

The distribution of mosses in various situations was not determined in detail, but differences did not appear to be so marked as in the case of higher plants. It is probable, however, that several mosses are excluded from town walls bordering busy streets by the

accumulation of dust. The following species were listed from six such walls, the number of records also being given:

Tortula muralis	6	*B. caespiticium*	4
Ceratodon purpureus	5	*Barbula vinealis*	3
Bryum argenteum	5	*Bryum capillare*	1

Even in shaded situations, pleurocarpous mosses are very rare on such walls.

4. SUCCESSION

Few detailed observations have been made on the progressive changes undergone by wall vegetation, but the general course follows that described by Amann (1928). Pioneers in dry situations are crustaceous lichens and cushion-forming mosses such as species of *Grimmia* and *Tortula*, which are able to colonize bare brick and stone surfaces. In damper situations, such as wall bases, certain algae probably play a part in this primary colonization. In exposed situations, the process may be arrested here but, under favourable conditions, other mosses requiring a certain accumulation of humus become established. Seedlings of ubiquitous wall plants such as *Poa annua* and *Linaria cymbalaria* frequently appear at this stage. If, in addition, shaded positions are available, pleurocarpous mosses such as *Hypnum cupressiforme* in turn colonize the moss carpet and eventually replace the original pioneers. On horizontal ledges, humus may accumulate to a depth of about 5 cm. and a final stage is reached where flowering plants, including seedling trees, form a more or less continuous cover (Pl. 19, phot. 5). Colonization by flowering plants and ferns is, however, not always dependent on the previous growth of mosses and can take place directly, even on vertical walls, provided that there are small cracks.

Flowering plant seedlings established in thin moss carpets may have a high rate of mortality. In one patch of *Tortula muralis* about 40 cm. square, kept under observation in 1939, seedlings first germinated in early March. They continued to appear steadily until mid-April, when there was a considerable increase in numbers: by early May, 39 seedlings of six species had developed. All these, however, were killed within a few days by the onset of dry weather in mid-May.

The rate of spread of mosses varies considerably with position. On a shaded stone parapet, *Tortula muralis* spread just over 2 cm. in one year and two other mosses colonizing it, *Barbula vinealis* and *Brachythecium rutabulum*, spread 2 and 3·5 cm. respectively. On an exposed brick-wall top, however, the average yearly growth of *Tortula muralis* was estimated to be about 0·5 cm. Again, *Camptothecium sericeum* grew 1·6 cm. in one year on the north ledge of Trinity College bridge, but only 0·6 cm. on the south ledge. By way of comparison, a plant of *Linaria cymbalaria* grew 35 cm. along an unshaded brick wall in a year.

pH measurements suggest that mosses which colonize bare stone may accumulate humus of about neutral reaction over an alkaline substratum. Thus a value of 8·2 was obtained from the bare stone of one building and a value of 6·8 from humus formed under *Camptothecium sericeum* in a comparable situation. The colonization of brick, however, does not appear to lead to significant changes in the pH level, which initially is in the region of 7·0–7·5.

An interesting small-scale succession is sometimes shown by cushion-forming mosses on the vertical sides of old walls. In the early stages, *Tortula muralis* colonizes the uneven surface of the mortar or larger depressions in the bricks themselves, the colony being

more or less crescent-shaped. There is a steady increase in size, and horizontal spread frequently leads to the fusion of neighbouring colonies; towards the base, however, the moss soon loses vigour. *Bryum argenteum* sometimes becomes established in the upper part of a colony but never becomes dominant. *Barbula vinealis* and *Ceratodon purpureus*, on the other hand, frequently become dominant after colonizing the *Tortula*, so that several older moss cushions have an actively growing crest of *Barbula* or *Ceratodon* and a marginal growth of *Tortula*. When they have attained a thickness of 1·0–1·5 cm., the cushions gradually peel off, often pulling out a considerable amount of mortar from the wall.

A similar succession may be seen on the sloping stone tops of other walls, where *Tortula muralis* forms an almost continuous mat. *Bryum argenteum* colonizes this to a considerable extent but never becomes dominant, whereas *Ceratodon purpureus* becomes completely dominant locally. The *Ceratodon* mats tend to break away from the stone after reaching a thickness of about 2 cm. and colonization by *Tortula* starts again. Numerous differences of detail are to be found in these cyclic successions, but the general pattern is similar.

Instability of moss cover may also result from the overgrowth of other plants. Crustaceous lichens sometimes grow over moss colonies, which then lose vigour and break away from the wall (Pl. 19, phot. 6). This often takes place on walls shaded by trees, but the factors which favour the invasion of lichen are not understood.

Although the interaction of plants brings about changes in wall vegetation, interference by man and by birds is undoubtedly a major factor affecting succession. Birds often remove moss from wall tops and ledges, and this helps to explain the patchwork of cushion and creeping mosses found in places frequented by birds. Seedling trees cause considerable damage to walls and stonework and are frequently removed before they grow more than 0·5 m. high. Higher walls tend to be relatively undisturbed, however, and trees of a considerable age are sometimes seen on them. It follows from the account already given of the effect of moisture and colonization (p. 142) that different stages of succession may be found on various parts of a wall. Rain flowing off the top of a wall may allow the establishment of moss on the highest part of the vertical sides. In this region, however, weathering is rapid and repointing often becomes necessary. Many old walls, therefore, now have a later stage of succession half-way down the sides than they have at the top. The moss cover of a brick wall top is shown in Pl. 18, phot. 4; the contrast between the original wall and the repointed section is clear.

5. Summary

An account is given of the wall flora of the Cambridge district. Of the 186 vascular plants recorded, 49 % were hemicryptophytes, 27 % therophytes and 15 % phanerophytes, the majority of the last probably being of garden origin. Most of the plants were dispersed by wind, but nearly half of them had no particular modification assisting such dispersal.

Many interrelated factors influenced the colonization and growth of wall plants. One factor was the type of building material and state of weathering of the wall. The supply of moisture tended to limit plant growth to the tops and bases of walls and to ledges. When water overflowed intermittently from a pipe or some other source, plants frequently colonized the vertical sides also. Several riparial species were present on river walls, usually at 10–15 cm. above the summer water-level. Plant communities on the north and

south sides of walls were often markedly different in composition and density. In many instances, scattered colonies of cushion-forming mosses were present on the north side and a dense mat of pleurocarpous mosses on the south. Several wall plants were found to have a preference either for sunny or for shaded positions. The wall flora tended to vary with situation: a roadside wall in the centre of the town, for example, had only one species common to a similar wall in a residential area. The influence of short-distance dispersal was considerable.

Crustaceous lichens and cushion-forming mosses were the pioneer plants in dry situations, and certain algae probably played a part in the primary colonization of damp walls. Where the site was not too exposed, slow accumulation of humus led to colonization by other mosses and by seedlings of flowering plants. Flowering plants frequently became established without the previous growth of mosses, however. Small-scale cyclic successions were shown by mosses in some situations. Birds, by the removal of moss, and man, by the removal of seedling trees and the repointing of walls, markedly influenced plant succession.

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THE POPULATION OF BURIED VIABLE SEEDS IN RELATION TO CONTRASTING PASTURE AND SOIL TYPES

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(With nine Figures in the Text)

Studies relating to the population of viable seeds buried in the surface layers of the soil are a relatively recent development. Brenchley & Warington (1930, 1933, 1936 and 1945) were among the first to study the question of buried viable seeds under arable conditions, at Rothamsted and Woburn. This was followed by the work of Chippindale & Milton (1934) and that of Milton (1936, 1939 and 1943) at Aberystwyth and at Stratford-on-Avon. These writers devoted their studies to viable seed in soils underlying pastures. The present report also deals with the soils beneath grassland but the authors have had the opportunity of greatly extending the range of soils as well as of pasture types under examination.

Samples were taken from a number of selected fields in different parts of England. The majority of these samples were from fields that had been critically studied during the Grassland Survey of England and Wales made by Stapledon & Davies (1945). The selected fields were chosen to represent a wide range of grassland types. Most of the fields under examination in different parts of the country were in grass in 1940. By 1944 when these were sampled for buried seeds, some of the fields had been ploughed for wartime cropping and a few had carried as many as three arable crops. There were some where a ley had been established in the intervening years. Some of the samples examined were collected from fields under detailed observation by the Station in connexion with its animal live weight production trials. There were also a few samples from fields on the Grassland Improvement Station farm. These latter represented a second examination of a number of fields already investigated by Milton (1943).

In the report there are two parallel sets of observations. The fields in grass are considered under their grassland types. Arable and ley fields are classed together as arable types and fitted into the grassland classification according to their 1940 grass condition. A few samples such as 'derelict arable' and 'worn-out leys' could not be fitted into the general classification and are therefore treated separately.

The classification of grassland which has been adopted is that of Davies (1941). The number of samples examined and the type of grassland they represent are shown in Table 1. The groups are subdivided into lowland, downland (including Cotswold) and upland (over 1000 ft.). In the lowland group, the only fescue field which was investigated contained a fair proportion of *Agrostis*. This field is, therefore, hardly typical of the group, but it has been retained in this section as it was the nearest approach to a lowland fescue that was available.

In addition to the main series, a large number of samples were collected on fields at Colesbourne (Gloucestershire) and Mixon Hay (Staffordshire), the two wartime sub-stations of the Grassland Improvement Station. Colesbourne lies on the Cotswold Hills where the soil is a light oolitic brash. Mixon Hay stands at an elevation of 1200 ft. and

upward on the fringe of the Peak district: the soil is loamy and characteristically acid overlying in the main the millstone grits, although there is some which overlies derivatives of the carboniferous limestone series.

On fields under grass, samples were taken from the top 2 in. of turf using an ordinary bulb planter with a diameter of 2·2 in. Wherever the depth of soil allowed, a further 4·5 in. was removed, using a longer borer similar to the type used by Milton (1936) in which the distal end of the metal part is graded away to a blunt point. This has the

Table 1. *Classification of fields sampled for buried seeds—based on Grassland Survey of England and Wales* (*Davies,* 1941)

The table shows the total number of fields sampled of each type. The arable fields are classified separately according to their 1940 grass condition. In the 'grouped' types the lowland, downland and upland figures are summated. They are given separately as 'divided' types. The various moorland associations are represented by a single set of figures in the 'grouped' types. l., lowland 'divided' types; d., downland 'divided' types; u., upland 'divided' types.

Type of grassland	Grassland (number of samples)				Arable (number of samples)*			
	Divided types			Grouped types	Divided types			Grouped types
	l.	d.	u.		l.	d.	u.	
(1) 1st grade ryegrass pasture >30% ryegrass	2	.	.	2	2	.	.	2
(2) 2nd grade ryegrass pasture 15–30% ryegrass	3	.	.	3	4	.	.	4
(3) 3rd grade ryegrass pasture <15% ryegrass	3	2	.	5	.	.	.	.
(4) *Agrostis* pasture	5	1	4	10	4	.	.	4
(5) *Agrostis*-fescue pasture (including tor-grass pastures)	1	.	2	3	2	.	.	2
(6) *Agrostis* with rushes and sedges (also pure rushes)	1	.	2	3	.	.	.	.
(7) Fescue pasture	1	3	2	6	2	1	.	3
(9) Moorland: *Nardus*	.	.	2					
(10) *Molinia*	.	.	1					
(11) Cotton-grass	.	.	1	6				
(12) Heather-moor	.	.	1					
Mixed (*Nardus, Molinia,* cotton-grass and heather)	.	.	1					
Samples that do not fit into Grassland classification description of type								
Worn-out ley	2	.	.	2	.	.	.	.
Worn-out ley cultivated	.	.	.	.	2	.	.	2
Old arable now in ley	.	.	.	.	1	.	.	1
Old arable	.	.	.	.	1	.	.	1
Derelict arable	.	.	.	.	2	.	.	2
Totals	18	6	16	40	20	1	0	21

* Fields ploughed since 1940 classified according to 1940 grass type.

disadvantage that the bottom of the borer does not hold a full core and therefore the lowest 1·5 in. of soil has always to be discarded. Chippindale & Milton (1934) suggest that these lower layers are unlikely to contain many viable seeds. In some instances stones blocked the passage of the borer when sampling; in such cases sampling was to a depth only of 2·5–3·5 in. Where cultivations had already caused a thorough mixing of the soil at the different levels it was of no special interest to separate 'top' and 'under' samples; here only the longer borer was used. The samples were taken to a depth of 7 in. The number of borings varied from fifteen to forty per field, the precise number depending upon the size of the field.

The main series of fields were sampled between mid-July and late October 1944. The samples were dried in the glasshouse in order to kill as much vegetative matter as possible. In March 1945 sub-samples (equal to half the original samples) were put to germinate on a layer of sand in wooden boxes. The sand was from 0·5 to 1 in. deep, and the depth of the soil varied from 1 to 1·5 in. 'Top' and 'under' soil samples were kept in separate boxes. The boxes were watered on 7 March and kept moist for 4 months. During this period the seedlings were removed and counted as soon as they were large enough to be identified. The first seedlings were removed on 21 March, a fortnight after the boxes were first watered. A record was also kept of seedlings that germinated in the previous autumn (1944) while the soils were drying out.

Most of the samples were contaminated during the winter 1945-6,* it was therefore impracticable to continue the experiment over a second year. However, germination was continued through the 1946 season in a few samples selected because the risk of any contamination could be entirely discounted. These gave an indication of the percentage of viable seeds that had germinated in the first season. Results will be discussed later.

The fields from the sub-stations at Colesbourne and Mixon Hay were sampled earlier than the main series. Some of these sub-station samples were taken in 1942 and the remainder in 1943. These samples remained in the greenhouse for two seasons, but the figures for the first season only have been used so that they should be compared with those of the main series.

RESULTS

A. *Consideration of the data obtained from the different grassland and arable types*

The number of seedlings removed from the 'top' and 'under' samples were added together to give one set of figures for each field. In doing so, it was noticed that germination was consistently greater in the 'top' soil than in the 'under' soil. The number of plants of each species and the resulting populations in millions per acre were tabulated separately for each field. These were combined to produce similar tables for each type of grassland and corresponding arable. Summaries only of these tables are presented (Table 2). The first part shows the average, maximum and minimum number of species; the remainder of the table contains similar figures for the average, maximum and minimum populations. 'Grouped' types where the lowland, downland and upland figures are summated are to be differentiated from 'divided' types where these are given separately. In the 'grouped' types the various moorland associations (types 9–12 and mixed-moor) are represented by a single set of figures.

Some of these data are presented graphically (Figs. 1A, B and 2A, B) 'A' refers to 'grouped' and 'B' to 'divided' types. Arable figures do not appear in the graphs and the type 'worn-out ley' is also omitted as this does not fit into our grassland classification. Figs. 1A, B refer to the average total number of species while Figs. 2A, B show average total populations. The data covered by Figs. 1 and 2 are linked together in Figs. 3A, B which refer to the average number of plants of each species, or the population:species ratio.

The salient features of Table 2 and Figs. 1–3 are described below. When considering these data it must be noted that the number of fields in each group varies, so that the value of data representing the mean of the fields in any one type also varies. Unfortunately, some types are represented by only a single field.

* These soils were contaminated during the removal of the Station from Dodwell to Drayton.

Table 2. *To show the total population of buried viable seeds in the soil underlying several grassland and arable types under investigation. Samples collected chiefly in 1944 (Colesbourne and Mixon Hay samples 1942/3). Populations determined by aggregate germination induced in first complete season following sampling*

Populations in millions per acre. l., lowland; d., downland; u., upland; G., grassland; A., arable at time of sampling.

Type classified according to grassland survey		No. samples		Average no. species		Maximum no. species		Minimum no. species		Average population		Maximum population		Minimum population	
		G.	A.	G.	A.	G.	A.	G.	A.	G.	A.	G.	A.	G.	A.
(1) >30 % ryegrass	l.	2	2	17	6·5	18	7	16	6	21·73	2·00	21·95	2·06	21·51	1·94
(2) 15–30 % ryegrass	l.	3	4	23	15·2	27	24	19	11	28·65	22·58	44·90	42·36	18·33	10·59
(3) <15 % ryegrass	l.	3		27		32		20		40·99		71·37		21·65	
	d.	2		33		40		26		27·97		31·26		24·69	
	Total l.+d.	5		29·2		40		20		35·98		71·37		21·65	
(4) *Agrostis*	l.	5		24·2		41		19		33·7		60·55		15·12	
	d.	1		54						40·88		66·30		20·39	
	u.	4		29·7		38		24		36·58					
	Total l.+d.+u.	10	4	30·2	9	54	15	19	4	34·99	16·94	66·30	49·24	15·12	1·80
(5) *Agrostis*/fescue including tor-grass	l.	1		31		39		25		40·49		72·16		70·68	
	u.	2		32						71·42				40·49	
	Total l.+u.	3	2	31·7	16	39	19	25	13	61·11	28·02	72·16	47·77		8·27
(6) Rushes	l.	1		27		16		10		62·68		75·05		2·02	
	u.	2		13		27		10		38·53				2·02	
	Total l.+u.	3		17·7		27		10		46·58		75·05			
(7) Fescue	l.	1		12		39		16		25·92		32·53		4·44	
	d.	3		30		34		23		20·02		82·15		18·37	
	u.	2		28·5						41·07					
	Total l.+d.+u.	6		25		39		12		27·02		82·15		4·44	
	l.		2		8		13		3		11·31		21·62		0·99
	d.		1		21						7·92				
	Total l.+d.		3		18·3		21		3		10·18		21·62		0·99
(9) *Nardus*	u.	2		19·5		24		15		31·26		32·71		29·80	
(10) *Molinia*	u.	1		15						8·07					
(11) Cotton grass	u.	1		11						10·05					
(12) Heather	u.	1		7						59·36					
Mixed-moor	u.	1		25						30·50					
Total moorland types	u.	6		16		25		7		28·42		59·36		8·07	
Worn-out ley	u.	2		11·5		13		10		13·02		15·73		10·33	
Worn-out ley after cult.			2		16·5		17		6		15·01		20·95		9·57
Old arable now in ley			1		10						29·60				
Old arable			1		2						1·12				
Derelict arable			2		27		30		24		53·63		86·91		20·45

Graphs (Figs. 1–3) summarizing the buried seed populations and the number of species recorded from different types of grassland.
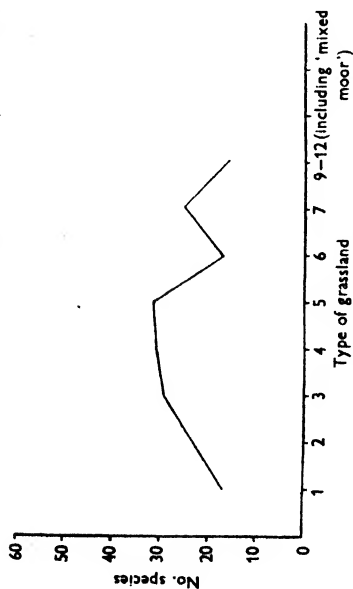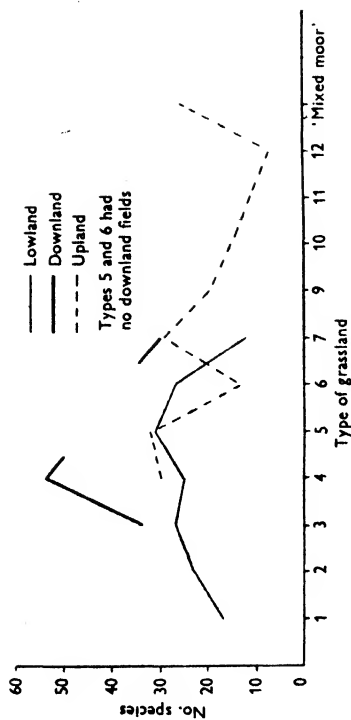

Fig. 1 A. [No. species (grouped types).

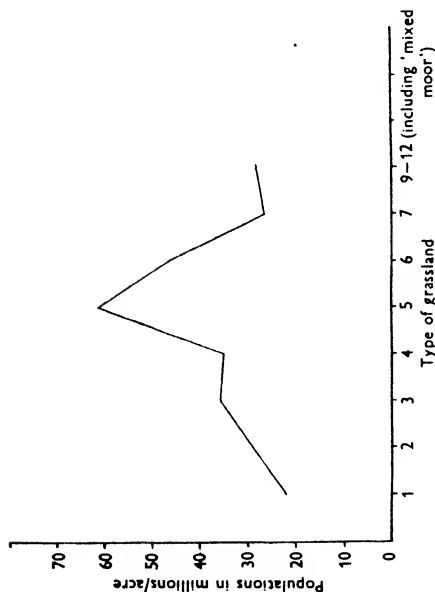
Fig. 1 B. No. species (divided types).
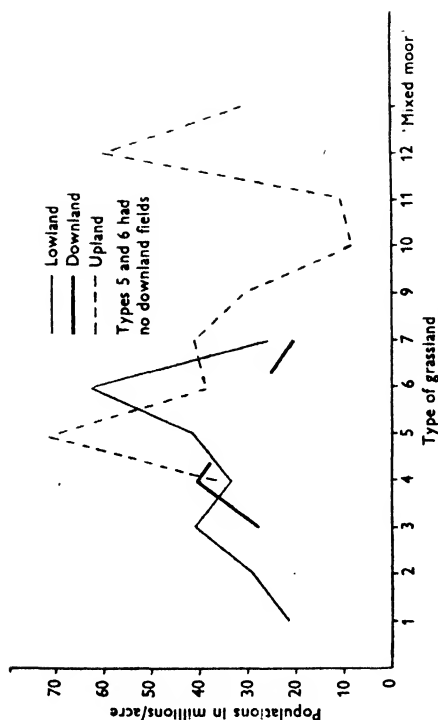

Fig. 2 A. Populations in millions/acre (grouped types).

Fig. 2 B. Populations in millions/acre (divided types).

(*a*) A general increase is found in both the number of species and in the populations of viable seeds from first-grade ryegrass pastures (type 1) to *Agrostis*-fescue (type 5). This increase is irregular: *Agrostis* (type 4) tends to form a trough.

(*b*) The population:species ratio is almost constant over the range types 1–4 (first-grade ryegrass to *Agrostis*).

(*c*) Rush associations (type 6) have few species, but high populations. The population:species ratio is very high.
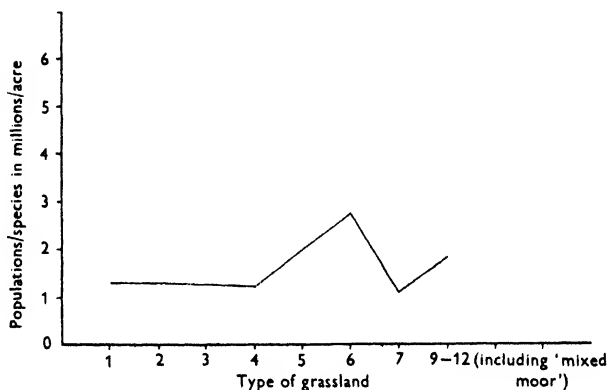
Fig. 3A. Populations/no. species (grouped types).
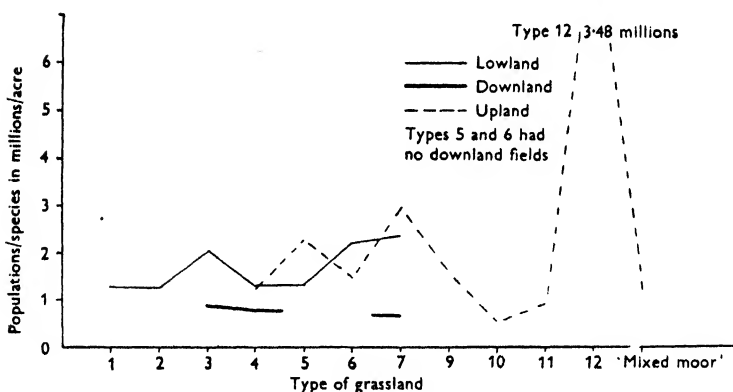
Fig. 3B. Populations/no. species (divided types).

(*d*) Fescue pastures (type 7) tend to have low populations and a low population:species ratio. When considering the grouped figures it must be remembered that downland fields make their maximum contribution in this type: three out of a total of six fields are downland.

(*e*) The average number of species and populations for the moorland types are low, but the 'divided' types show a considerable variation between the different moorland communities and also between the other upland types. The high population:species ratio for heather-moor is emphasized by the abnormally high population (56 million) of one single species (*Calluna*).

(*f*) The ratio population:species for downland is well below that for lowland or upland.

(g) Arable figures are consistently lower than those for grassland. Hence it would appear that a few years' cultivation tends to reduce both the variety and the quantity of the potential weed population. The arable and grass populations also differed somewhat in character, although no marked difference in the percentage distribution between grasses, legumes and 'other species' is apparent in the data (Table 3). Many arable populations included a large proportion of recently sown herbage species and therefore actual populations of weeds are well below the figures given.

(h) The lower section of Table 2 illustrates the marked difference exhibited between the low buried seed populations of the 'old arable' soil and the very high content of the 'derelict arable' fields. Although the 'old arable' figure represents only one field and is probably abnormally low, these results suggest that 'derelict arable' fields contain more weed seeds than fields under an efficient system of cultivation. The 'old arable now in ley' field, which was put down to grass in 1939 gave a much higher population than the 'old arable' field, but the figures are still below those for 'derelict arable'.

Table 3. *To show the distribution between grasses, legumes and 'other species' of the number of species and the populations of viable seeds in non-calcareous and calcareous soils under investigation*

	No. species (% composition)			Populations (% composition)		
	Grasses	Legumes	Other species	Grasses	Legumes	Other species
Non-calcareous soils:						
Lowland grass	37	9	54	56	13	31
Lowland arable	38	17	45	57	7	36
Upland grass	42	5	53	48	2	50
Calcareous soils:						
Lowland grass	31	6	63	37	4	59
Lowland arable	36	3	61	63	12	25
Downland grass	27	8	65	32	11	57
Downland arable (single field)	33	10	57	60	18	22

Table 3 shows the percentage distribution between grasses, legumes and 'other species' of both the number of species and the populations of viable seeds in calcareous and non-calcareous soils. Separate figures are given for arable and grass. Calcareous soils are here represented by the downland fields and the calcareous Lias clay at the Station. The legumes found on calcareous soils are of particular interest since a wide variety of legumes is characteristic of calcicolous communities. The figures shown (Table 3) do not suggest that calcareous soils contain a significantly higher proportion of legume viable seeds than non-calcareous soils.

B. *Comparison between seeds buried in the soil and the botanical composition of the sward*

The results of the present survey have, in general, substantiated the earlier conclusions reached by Milton (1936, 1939). For example, *Agrostis*, *Calluna* and *Juncus* are usually heavily represented in the viable seed populations, while *Cirsium arvense*, *Molinia*, *Nardus* and *Eriophorum* either produce few seeds, or some other factor may be at work which inhibits seed preservation in the soil. Evidence from this survey is in support of this and is illustrated by a comparison of the buried seed figures with the composition of the overlying sward in respect of the five fields examined (Table 4). Both botanical composition and the buried seed populations are given in terms of percentage composition. The

Table 4. *To show the percentage composition of the viable buried seed flora compared with the composition of the overlying herbage in a number of representative fields*

(N.B. Minor species are omitted in this table)

	Fields									
	Class 1 Leicestershire old pasture		Class 3 Field 27 (Colesbourne)		Class 4 Field N1 (Mixon Hay)		Class 7 Field 15 (Colesbourne)		Class 10 *Molinia* moor (Somerset)	
Species	% cover of turf	% population (buried seeds)	% cover of turf	% population (buried seeds)	% cover of turf	% population (buried seeds)	% cover of turf	% population (buried seeds)	% cover of turf (rough analysis only)	% population (buried seeds)
GRASSES:										
Agrostis spp.	5	**21**	21	**25**	36	**62**	.	**15**	.	**6**
Alopecurus pratensis	0·5	0·5	.	T	6	3	.	1	.	.
Anthoxanthum odoratum	.	.	T	0·5	3	2	.	.	.	.
Brachypodium pinnatum	.	.	.	.	.	.	18	.	.	.
Briza media	.	.	.	.	.	.	T	2	.	.
Bromus erectus	.	.	.	.	.	.	35	.	.	.
Cynosurus cristatus	6	.	1	2	.	T	.	.	.	.
Dactylis glomerata	.	.	18	1	4	0·5	.	.	.	5
Deschampsia caespitosa	.	.	T	0·5	8	2	.	1	.	.
Festuca ovina	.	.	.	0·5	11	0·5	T	0·5	.	.
F. pratensis	.	.	2	.	.	.	.	.	.	.
F. rubra	.	.	11	.	T	0·5	5	.	T	1
Holcus lanatus	1	.	4	4	.	1	T	.	.	.
H. mollis	.	.	.	.	21	.	.	.	.	.
Lolium multiflorum	.	.	T	.	1	T	.	.	.	.
L. perenne	44	0·5	10	1	.	3	.	.	.	2
Molinia caerulea	.	.	.	.	.	.	.	.	50–60	.
Phleum pratense	9	.	2	.	.	.	.	.	.	1
Poa annua	T	**21·5**	.	.	.	2	.	3	.	.
P. pratensis	0·5	1·5	.	2	6	1	3	**16**	.	.
P. trivialis	**10·5**	4	5	**9**	.	3	.	**6**	.	3
LEGUMES:										
Lotus corniculatus	T	.	1	.	.	.	4	**16**	.	.
Medicago lupulina	.	.	.	.	.	.	T	3	.	2
Trifolium pratense	.	.	2	0·5	.	.	T	.	.	.
T. repens	13	**24**	6	**9**	T	0·5	.	.	.	3
OTHER SPECIES										
Calluna vulgaris	.	.	.	.	.	.	.	.	1	.
Carex spp.	.	.	T	T	.	.	2	.	.	.
Centaurea spp.	.	.	T	0·5	.	.	3	.	.	.
Cerastium vulgatum	T	1	T	**16**	T	T	.	2	.	.
Cirsium spp.	T	.	.	.	.	.	9	.	T	.
Erica spp.	.	.	.	.	.	.	.	.	T	1
Eriophorum polystachion	.	.	.	.	.	.	.	.	· 0·5	.
Galium spp.	.	.	.	.	1	3	1	0·5	.	.
Juncus spp.	.	.	T	0·5	T	**7**	.	0·5	15	**68**
Leontodon spp.	.	.	2	T	.	.	3	.	.	.
Linaria minor	.	.	.	.	.	.	4	.	.	.
Luzula campestris	.	.	T	T	T	0·5	.	0·5	.	.
Plantago spp.	.	4	3	4	T	.	1	.	.	.
Potentilla spp.	.	.	.	.	.	.	.	4	T	.
Poterium sanguisorba	.	.	.	.	.	.	5	T	.	.
Prunella vulgaris	.	.	.	2	.	.	.	.	.	.
Ranunculus spp.	1	**7**	3	**8·5**	T	2	.	T	.	.
Rumex spp.	.	.	3	0·5	T	.	.	.	.	.
Scirpus spp.	.	.	.	.	.	.	.	.	20	.
Senecio vulgaris	.	1·5	T	0·5	.	5	.	9	.	.
Sonchus spp.	.	.	.	.	.	1	.	5	.	6
Stellaria media	.	.	.	0·5	.	.	.	.	.	1
Taraxacum officinale	T	1	T	0·5	.	.	.	.	.	.
Urtica dioica	.	**9**	.	.	.	T	.	T	.	.
Other species	9·5	3·5	6	11·5	3	0·5	12	10	Approximate analysis only	1
Total	100	100	100	100	100	100	100	100		100

botanical composition is based on the estimated percentage area cover while the seed data refer to the number of seedlings. Where any species shows a wide contrast in relation to its contribution to either set of data (sward composition or seed population) this higher figure is in black type.

Reference to Table 4 shows also that the following species are among those which exhibited a markedly higher percentage of buried viable seeds than would be expected from the botanical composition of the sward.

<div align="center">Group A</div>

Grasses	*Agrostis* spp.	Other species	*Cerastium vulgatum*
	Poa annua		*Juncus* spp.
	P. pratensis		*Potentilla reptans*
	P. trivialis		*Ranunculus* spp.
Legumes	*Lotus corniculatus*		*Scirpus caespitosus*
	Medicago lupulina		*Senecio vulgaris*
	Trifolium repens		*Sonchus* spp.
			Urtica dioica

The figures for *Poa pratensis* (smooth-stalked meadow grass) and *P. trivialis* (rough-stalked meadow grass) are most variable but they still fit into this group. *Calluna vulgaris* (ling) was recorded in only one of the fields compared in Table 4. Here it accounted for 1% of the herbage, but we found no viable seed in our samples. The results of other fields, however, suggest that *C. vulgaris* might also be included in this group. In mixed-moor, for example, *Juncus effusus* (13·53 million) was the only species to give more seeds than *Calluna* (5·28 million).

The following species contributed a higher percentage to the herbage than to the buried seed populations:

<div align="center">Group B</div>

Grasses	*Brachypodium pinnatum*	Grasses	*Lolium perenne*
	Bromus erectus		*Molinia caerulea*
	Dactylis glomerata		*Phleum pratense*
	Deschampsia caespitosa	Other species	*Cirsium* spp.
	Festuca ovina		*Eriophorum polystachion*
	F. pratensis		*Leontodon* spp.
	F. rubra		*Rumex* spp.
	Holcus mollis		

The evidence for *Eriophorum* (cotton-grass) in Table 4 is inconclusive but is corroborated by the very small seed population of this species found in the cotton-grass moor and the 'mixed-moor'.

Low seed populations of *Lolium perenne* (ryegrass) were general but there were exceptions. The sample from the Sedgemoor meadows, Somerset, was outstanding; its ryegrass population approached 9 million of viable seed per acre. This was slightly greater than the *Juncus* (rush) population and over twice as great as that of *Carex* (sedge), although ryegrass was not represented in the herbage growing on the field concerned.

The principal species that cannot be classed in either of the foregoing groups A and B are listed below (group C). The data in respect of these plants are variable and show frequently only a small difference between their proportions in the herbage and in the viable seed.

<div align="center">Group C</div>

Grasses	*Alopecurus pratensis*	Other species	*Carex* spp.
	Anthoxanthum odoratum		*Galium* spp.
	Cynosurus cristatus		*Luzula campestris*
	Holcus lanatus		*Plantago* spp.
	Lolium multiflorum		*Taraxacum officinale*
Legumes	*Trifolium pratense*		*Veronica* spp.

Some of the species listed above were present only in small quantities. It is possible that further studies will show these and other species to have marked trends towards groups A or B.

An interesting feature of these comparisons is the proportions of grasses, legumes and 'other species' in the different groups. The proportion of grasses is very high in group B and that of 'other species' is correspondingly low, while group A is largely composed of other species and legumes with very few grasses. Thus it can be seen how miscellaneous species often take a disproportionately important place in relation to the population of viable seeds buried in the soil. Many of the herbs of our grasslands may give a very high buried seed population and yet occur as no more than occasionals in the pasture.

C. *Occurrence of the individual genera and species*

In the summary of the data for each species (Table 5) the results from the 'grass' and 'arable' samples are treated separately. The number of 'grouped' types and the total number of fields on which the individual species was found are given in the first two columns. The next section shows the number of these fields divided into lowland, downland and upland. The maximum population is given as well as the number of populations falling within each of the following frequency groups: <0·5 million, 0·5–1·0 million, 1–2 million, 2–10 million and >10 million. These divisions differ from those used by Milton (1936, 1943) and have been introduced to emphasize the high populations. Unfortunately, the distribution of the species between the different types of grass or arable had to be omitted; it was felt that the inclusion of these data, even in a qualitative form, would make this section too cumbersome.

A few genera and species, however, are considered below in some detail. The plants chosen are agriculturally important and have been selected from a variety of habitats.

(a) *Agrostis*. The average *Agrostis* populations on the grassland types are represented in Fig. 4. *A. tenuis* was the chief contributor and occurred on thirty-three fields (five grassland types 'grouped'). It is also likely that much of the *Agrostis* (species not determined) also belonged to *A. tenuis* (brown-top). *A. canina* was found in upland samples only.* The form of the graph is remarkable because the populations of *Agrostis* decline from first- to third-grade ryegrass pastures (types 1–3); this is inversely proportional to the occurrence of *Agrostis* in the sward. The lowland populations increase from type 3 and reach a maximum on type 7 (fescue). Thus the lowland *Agrostis* figures for viable seed bear little relation to the percentage of that grass in the sward. Both the downland and the upland results follow the herbage composition more closely. Viable buried seed of *Agrostis* occurred erratically on the arable types, it was recorded in twelve out of the twenty-one 'arable' fields. The two outstanding 'arable' populations (25 and 19 million respectively) were both recorded at the Grassland Improvement Station land which was completely derelict prior to 1940.

(b) *Lolium perenne*. The populations of *Lolium* were usually low but the variations are difficult to interpret. The species has a marked lowland bias, since it occurred on fourteen out of eighteen lowland fields, four out of six downland and only eight out of sixteen upland grass fields. The populations varied from 0·07 to 8·72 million per acre. It is of

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* The unidentified *Agrostis* from two downland fields was originally thought to be *A. canina* but its identification was not absolutely certain. *A. canina* was not recorded among the herbage of these downland fields, so it was thought best to classify these seedlings as 'unidentified' *Agrostis*.

interest to note that two of the lowest populations (0·08 and 0·11 million) were from the two first-grade pastures while a type 4 (*Agrostis*) field from Somerset had a ryegrass population of 6·47 million per acre. The population of 8·72 million from the Sedgemoor

Graphs (Figs. 4–9) summarizing the buried seed populations of a number of individual genera and species.
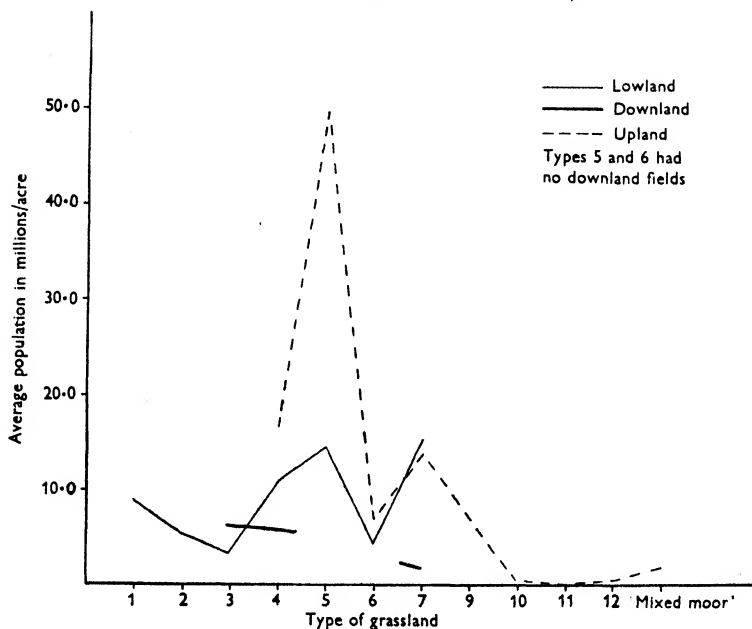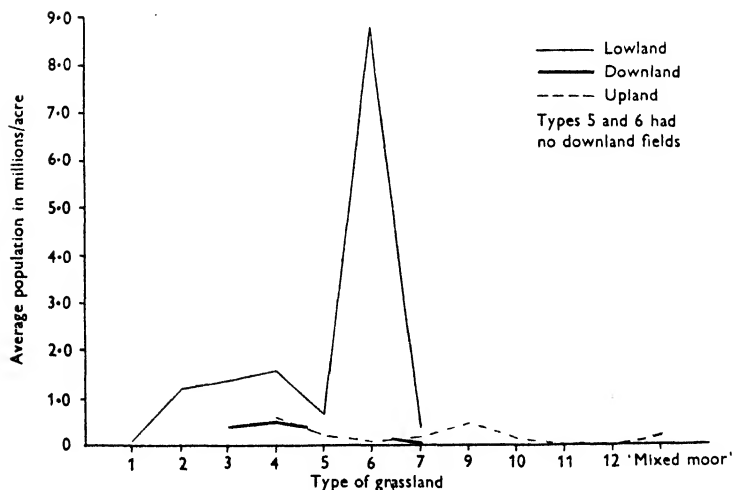

Fig. 4. *Agrostis* spp.

Fig. 5. *Lolium perenne.*

meadows in Somerset has been mentioned already. A possible explanation of these figures, which are shown graphically (Fig. 5) will be discussed later. Some of the 'arable' populations were very large but these came from fields that had previously been sown down to a mixture containing ryegrass. The indications here seem to point to the fact that some

Table 5. *Summary of the viable seed populations of individual genera and species and their distribution of the different types of grass and arable fields*

	Grassland											Arable										
			No. fields			Max. population in millions per acre	No. fields with populations (millions)					No. types (grouped)	No. fields	No. fields			Max. population in millions per acre	No. fields with populations (millions)				
Species	No. types (grouped)	No. fields (total)	Low-land (max. 18)	Down-land (max. 6)	Up-land (max. 16)		0–0·5	0·5–1·0	1–2	2–10	>10			Low-land (max. 20)	Down-land (max. 1)	Up-land 0		0–0·5	0·5–1·0	1–2	2–10	>10
GRASSES:																						
Agropyron repens (L.) Beauv.	4	4	·	3	·	14·30	·	·	1	1	1	1	1	·	·	·	0·22	1	·	·	·	·
Agrostis spp. (unidentified)	5	12	1	3	12	11·21	·	4	2	1	1	·	·	·	·	·	·	·	·	·	·	·
A. canina L.	2	2	2	·	·	1·32	4	1	1	·	·	·	·	·	·	·	·	·	·	·	·	·
A. gigantea Roth	1	1	·	1	·	0·33	1	·	·	·	·	·	·	·	·	·	·	·	·	·	·	·
A. alba L. var. Palustris	5	11	·	4	6	6·29	5	2	5	4	·	6	11	11	1	·	0·96	2	1	2	·	·
A. stolonifera L.	9	33	14	1	15	56·18	5	2	6	12	9	6	12	11	1	·	25·00	2	2	2	4	2
A. tenuis Sibth.	6	37	16	6	15	57·92	6	5	13	13	11	1	1	1	·	·	25·00	1	·	·	4	2
(Total Agrostis L.)	6	20	7	4	9	6·74	14	6	2	3	·	1	1	1	·	·	0·11	1	·	·	·	·
Alopecurus pratensis L.	8	19	6	2	11	2·97	11	3	4	1	·	1	1	1	·	·	0·13	1	·	·	·	·
Anthoxanthum odoratum L.	6	1	1	·	1	0·44	1	·	·	·	·	·	·	·	·	·	·	·	·	·	·	·
Arrhenatherum elatius L.	1	1	1	·	·	1·06	·	·	1	·	·	2	2	2	1	·	1·80	1	·	1	·	·
Avena sativa	1	1	·	1	·	0·54	1	·	·	·	·	·	·	·	·	·	·	·	·	·	·	·
Briza media L.	1	1	·	1	·	0·22	1	·	·	·	·	·	·	·	·	·	·	·	·	·	·	·
Bromus erectus Huds.	1	1	·	·	·	0·73	7	2	·	·	·	3	3	3	·	·	0·11	3	·	2	·	·
B. mollis L. sec. Holmbg.	6	9	3	2	4	3·76	11	·	1	2	·	3	3	3	·	·	0·36	8	·	·	·	·
Cynosurus cristatus L.	6	15	10	3	2	5·15	13	3	3	3	·	9	12	11	1	·	7·59	·	2	2	2	·
Dactylis glomerata L.	9	19	8	2	9	6·93	11	3	3	3	·	·	·	·	·	·	·	·	·	·	·	·
Deschampsia caespitosa (L.) Beauv.	7	20	3	4	13	0·50	8	1	·	·	·	·	·	·	·	·	·	·	·	·	·	·
D. flexuosa (L.) Trin.	4	9	·	2	7	2·09	7	·	1	1	·	1	1	1	·	·	0·33	1	·	·	·	·
Festuca ovina L.	5	8	3	2	6	1·80	3	2	2	1	·	·	·	·	·	·	·	·	·	·	·	·
F. pratensis Huds.	3	4	3	·	1	6·74	7	1	1	1	·	1	1	1	·	·	0·40	1	·	·	·	·
F. rubra L.	8	17	4	2	11	4·23	13	2	2	1	·	5	8	7	1	·	1·08	4	2	2	·	·
Holcus lanatus L.	8	28	14	3	11	0·90	11	8	8	4	·	2	2	2	·	·	1·15	2	·	1	1	·
Hordeum nodosum L.	5	6	3	1	2	8·72	4	2	·	5	·	5	6	5	1	·	3·24	2	1	1	3	·
Lolium multiflorum Lam.	8	26	14	4	8	4·89	16	5	5	2	·	7	14	13	1	·	15·46	5	2	1	4	2
L. perenne L.	6	10	7	1	2	12·27	6	2	2	5	1	3	4	4	·	·	33·78	4	3	1	2	1
Phleum pratense L.	6	22	12	2	8	5·16	5	6	4	5	·	7	11	11	·	·	25·42	4	3	1	·	·
Poa annua L.	7	20	6	5	9	31·98	12	4	2	2	1	4	4	3	1	·	1·44	3	·	1	2	·
P. pratensis L.	9	35	20	4	11	31·98	8	4	6	15	2	8	15	15	·	·	13·66	5	2	3	4	1
P. trivialis L.	9	37	18	6	13	32·35	8	1	4	17	7	8	16	15	1	·	28·19	2	5	2	4	3
(Total Poa spp. L.)																						
LEGUMES:																						
Lotus corniculatus L.	3	4	2	2	·	5·39	2	1	·	2	·	3	3	2	1	·	1·32	1	1	1	·	·
Medicago lupulina L.	5	10	4	5	1	2·03	5	·	3	1	1	2	2	1	1	·	0·36	2	1	·	·	·
Trifolium dubium Sibth.	4	9	5	2	2	14·38	7	1	1	1	·	2	2	1	1	·	0·72	4	3	·	·	·
T. pratense L.	5	12	8	3	1	1·15	10	1	1	·	·	3	3	2	1	·	8·31	8	1	·	3	·
T. repens L.	9	30	18	4	8	8·07	11	6	4	9	·	8	14	14	·	·	·	·	·	·	·	·
Ulex europaeus L.	1	1	1	·	·	0·08	1	·	·	·	·	·	·	·	·	·	·	·	·	·	·	·
Vicia sativa L.	1	1	·	1	1	0·37	1	·	·	·	·	1	1	1	·	·	0·36	1	·	·	·	·

OTHER SPECIES:

Species															
Achillea millefolium L.	2	2	1	2			1·35	1			1					1
Acinos arvensis (Lam.)	1	1	1	1			0·06									1
Arethusa cynapium L.	1	1	2				0·30	2	2	2			2	3		1
Alchemilla arvensis (L.) Scop.	1	2		2			0·25	2							1	
A. vulgaris L.	1	1	3	3			0·13	3								3
Anagallis arvensis L.	4	5					1·07						1	1	1	
Anthriscus sylvestris (L.) Hoffm.		1					0·06									
Apium graveolens L.	6	17	9	5	3		11·8	12	2	5	4		2	1		1
Bellis perennis L.	1	2	1	2			0·63	1	1	1			1	1		
Blackstonia perfoliata Huds.	1	1	1		2		1·34				1				3	
Brassica nigra (L.) Koch.	5	2	2				56·72	1						2		
Calluna vulgaris (L.) Hull		2	2	4	2		0·13	2	3	3		3	3	3		
Campanula rotundifolia L.	5	7	1				0·45	1								1
Capsella bursa-pastoris (L.) Medic.		1					0·22	1	1	1	2		1	1	1	2
Cardamine pratensis L.	6	13	3				3·40	10	3	3		2	3	3	1	
Carex spp. (unidentified)	2	3	3				0·24	3	3	3			1			
C. flacca Schreb.	2	3	1	1			0·13	3	2	1			2	2		
C. hirta L.	6	9	2	5			1·59	3	2	2		2	2	2		
C. panicea L.	6	20	6	9			3·40	5	2	5	3	3	5	5	1	5
(Total Carex	1	1		1			0·09	13								
Centaurea nigra L.	9	26	14	5	1		5·43	5	11	12	11	5	11	6		1
Cerastium arvense L.	1	1	1	1			0·06	1	1	1			1	1		
C. vulgatum L.																
Chamaenerion angustifolium (L.) Scop.																
Chenopodium album L.	5	7	5	2			0·90	5	5	6	5	5	5	4		1
C. polyspermum L.	4	1	1	1			0·13	1	1	2	2			2		
Chrysanthemum leucanthemum L.	4	7	5	2			1·70	7	2	2	3	2	2	1		
Cirsium arvense (L.) Scop.	1	1	5	1			0·13	1	1	1	1		1	1		
C. eriophorum (L.) Scop.	3	1	1				0·82	4	1	1						
C. palustre (L.) Scop.	3	4	1	1			0·18	2	1	1			1	1		1
C. vulgare Ten.	6	2	1				0·24	6	3	3	3	3	3	3		
(Total Cirsium Mill.		10	1	6			0·67	9								
Clinopodium vulgare L.	1	1	1				0·06	1								
Conopodium majus Lor and Barr.	1	1	1	1			0·60	1	1	1			1	1		1
Coronopus squamatus Aschers.	1	1	1				0·92	1								
Crepis capillaris (L.) Wall.	1	1	1				0·13	1					1	1		1
Daucus carota L.	1	1					2·08									
Erica cinerea L.	1	1	1	1			0·08	1	1	1	3	3	1	1		1
Eriophorum vaginatum L.	2	4	4	1			1·25	3								
Euphorbia exigua L.	1	1	1				0·06	1	1	1				1		
Fragaria vesca L.	1	1	1				0·18	1								
Fumaria officinalis L.	1	1	2	1			0·30	2								
Galium aparine L.	3	4	2				3·26	4	3	3	3	3	4	4	2	1
G. saxatile L.	5	11	5	9			1·20	7								
G. verum L.	1	6	3	3			3·26	10	3	3	3	3	3	1		
(Total Galium L.	1	1	1				0·25	1								1
Gentiana amarella L.	1	2	1	2			0·08	2	1	2	1		2	2	2	1
Geranium molle L.	2	3	1	1			0·85	1	1	1			2	2		
Hydrocotyle vulgaris L.	1	1					0·13	1						1		

Table 5 (continued)

Species	Grassland — No. types (grouped)	No. fields (total)	Lowland (max. 18)	Downland (max. 6)	Upland (max. 16)	Max. pop. in millions per acre	0–0·5	0·5–1·0	1–2	2–10	10	Arable — No. types (grouped)	No. fields	Lowland (max. 20)	Downland (max. 1)	Upland (0)	Max. pop. in millions per acre	0–0·5	0·5–1·0	1–2	2–10	10
OTHER SPECIES:																						
Helianthemum nummularium (L.) Mill.	2	2	.	2	.	0·13	2	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.
Hypericum perforatum L.	1	1	1	.	.	0·06	1	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.
Hypochoeris radicata L.	1	1	1	.	.	0·07	1	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.
Juncus spp. (unidentified)	5	18	3	2	13	11·69	10	4	.	2	2	.	.	.	.	.	.	.	.	.	.	.
J. articulatus L.	3	3	2	1	1	0·99	1	2	.	.	.	.	.	.	.	.	.	.	.	.	.	.
J. bufonius L.	6	13	5	1	7	7·19	11	.	.	2	.	.	.	.	.	.	.	.	.	.	.	.
J. communis Mey	6	17	3	.	14	33·70	5	3	3	4	2	1	1	1	.	.	0·72	1	.	.	.	.
J. effusus L.	4	7	4	2	1	1·02	6	.	1	.	.	.	.	.	.	.	.	.	.	.	.	.
J. inflexus L.	5	10	.	.	10	18·77	2	3	4	.	4	.	.	.	.	.	.	.	.	.	.	.
J. squarrosus L.	7	27	8	3	16	47·39	8	3	5	7	4	.	.	.	.	.	.	.	.	.	.	.
(Total *Juncus* L.)	7	.	8	2	16	.	8	1	5	4	4	1	1	1	.	.	.	1	.	.	.	.
Lamium purpureum L.	1	1	.	1	.	1·35	1	.	.	.	.	1	1	1	.	.	0·72	1	.	.	.	.
Leontodon autumnalis L.	1	1	1	.	.	0·60	1	.	.	.	.	.	.	.	.	.	0·17	1	.	.	.	.
L. leysseri Beck.	2	2	2	.	.	0·06	2	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.
L. hispidus L.	2	2	2	.	.	0·72	2	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.
Linum catharticum L.	1	1	1	.	.	0·25	1	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.
Linaria minor (L.) Desf.	2	3	1	.	.	1·28	1	1	.	1	.	1	1	1	.	.	.	1	.	.	.	.
L. spuria (L.) Mill	2	2	1	1	.	0·40	2	.	.	.	.	1	1	1	.	.	.	1	.	.	.	.
Luzula campestris (L.) DC.	5	19	5	2	12	1·25	13	5	.	.	.	2	2	2	.	.	0·71	2	.	.	.	.
Matricaria inodora L.	1	1	.	.	1	.	1	.	.	.	.	1	1	1	.	.	0·25	1	.	.	.	.
Myosotis arvensis (L.) Hill	1	1	1	.	.	0·13	1	.	.	.	.	2	2	2	.	.	0·60	1	1	.	.	.
Odontites rubra Gilip.	2	2	.	.	.	.	1	.	.	.	.	1	1	1	.	.	0·88	1	.	.	.	.
Papaver rhoeas L.	.	1	.	.	.	1·68	.	.	.	.	.	1	1	1	.	.	0·66	1	.	.	.	.
Pastinaca sativa L.	2	2	1	1	.	0·45	2	.	.	.	.	1	1	1	.	.	0·11	1	.	.	.	.
Plantago lanceolata L.	5	11	4	4	3	2·18	6	.	4	1	.	1	1	1	.	.	0·17	1	.	.	.	.
P. major L.	8	15	11	1	3	3·52	8	4	2	1	.	5	5	4	1	.	0·22	3	2	.	.	.
P. media L.	2	2	1	1	.	0·60	2	.	.	.	.	.	5	4	1	.	0·78	3	1	.	.	.
(Total *Plantago* L.)	9	22	14	3	5	3·52	11	4	4	3	.	5	6	5	1	.	1·54	3	2	1	.	.
Polygonum aviculare L.	2	5	3	2	.	0·26	5	.	.	.	.	3	4	4	.	.	0·88	2	2	.	.	.
P. convolvulus L.	2	2	1	1	.	0·45	2	1	.	.	.	3	5	4	.	.	1·48	3	1	1	.	.
P. persicaria L.	1	2	1	1	.	0·36	2	.	.	.	.	1	1	1	.	.	1·80	.	.	1	.	.
Potentilla erecta (L.) Rausch.	1	1	.	.	1	0·73	1	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.
P. reptans L.	4	6	2	3	1	4·17	1	1	1	1	.	3	5	4	.	.	0·61	3	2	.	.	.
Poterium sanguisorba L.	13	4	1	3	.	2·79	3	3	1	.	.	2	2	1	.	.	0·30	2	.	.	.	.
Primula veris L.	1	1	1	.	.	0·07	1	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.

Species																	
Prunella vulgaris L.																	
Ranunculus acris L.																	
R. bulbosus L.																	
R. ficaria L.																	
B. flammula L.																	
R. repens L.																	
R. sceleratus L.																	
(Total Ranunculus																	
Raphanus raphanistrum L.																	
Rhinanthus borealis Druce																	
Rubus caesius L.																	
Rumex acetosa L.																	
R. acetosella L.																	
R. crispus L.																	
(Total Rumex																	
Sagina apetala Ard.																	
S. procumbens L.																	
Sambucus nigra L.																	
Senecio jacobea L.																	
S. vulgaris L.																	
Sinapis arvensis L.																	
Solanum nigrum L.																	
Sonchus arvensis L.																	
S. asper (L.) Hill																	
S. oleraceus L.																	
(Total Sonchus L.																	
Spergula arvensis L.																	
Stellaria graminea L.																	
S. media (L.) Vill																	
Taraxacum officinale Weber																	
Thymus serpyllum L.																	
Thlaspi arvense L.																	
Urtica dioica L.																	
Valerianella locusta L.																	
Veronica agestis L.																	
V. beccabunga L.																	
V. chamaedrys L.																	
V. officinalis L.																	
V. serpyllifolia L.																	
(Total Veronica spp.																	
Viola hirta L.																	
V. palustris L.																	
V. tricolor L.																	

at least of the seed normally sown in mixtures tends to remain dormant in the soil, and yet to retain its viability.

(c) *The fine-leaved fescues* (*Festuca rubra* and *F. ovina*). These are also characterized by low populations. Fine-leaved fescues were recorded on all pasture types except types 1, 2, 7 (lowland) and type 11 (*Eriophorum*). Their absence on good ryegrass pastures is not surprising but the lowland fescue field is remarkable even though the field is not typical. Out of twenty fields on which the fine-leaved fescues occurred, seventeen had a population of less than 0·5 million per acre; of the remainder only two exceeded 2 million per acre. The maximum of 6·74 million seeds per acre was recorded on a type 6 upland (*Juncus*) soil. It is worth noting that the maximum *Lolium* and *Festuca* populations both occurred on soils under rushes (type 6). *F. ovina* (sheep's fescue) was confined to downland and upland samples, but *F. rubra* (red fescue) although showing an upland bias was less restricted; it was recorded on four lowland, two downland and eleven upland grass fields. These two fescues were each recorded on one arable field.

(d) *Medicago lupulina* (black medick). This legume shows a distinct downland bias; it was found in five out of six downland grass fields and also in one upland and four lowland samples. The maximum population (2·03 million) was on a lowland field (type 3) but three of the five downland fields had viable seed populations of over one million per acre. The single upland field in which it was recorded, the *Molinia* moor, produced only a small *Medicago* population (0·16 million).*
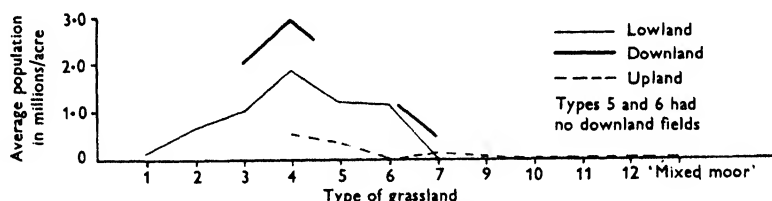
Fig. 6. *Cerastium vulgatum.*

(e) *Cerastium vulgatum* (mouse-ear chickweed). This very common weed was present in twenty-six 'grass' and twelve 'arable' fields with maximum populations of 5·43 and 7·91 million per acre respectively. On the upland field it was restricted to the better and drier types (types 4, 5 and 7). The downland populations were generally high as shown in the graph (Fig. 6).

(f) *Juncus* spp. Populations of *Juncus* were high but closely paralleled the ecological distribution of the genus; the populations were low on the better types of grassland and high in *Juncus* dominant communities (Fig. 7). Upland figures were higher than lowland or downland and the maximum population of 45·39 million occurred on an upland field in which the sward was dominated by rushes (type 6); of this population, 33 million were *J. effusus*. All ten fields where *J. squarrosus* was recorded were above 1000 ft. (upland). The genus was represented in only one arable field (type 2) and there the population was small (0·72 million).

(g) *Ranunculus*. The genus *Ranunculus* (buttercup) was remarkable for the close correlation between its ecology and its populations of buried viable seeds. Buttercups are typical grassland weeds and their seed occurred in twenty-nine out of forty grass fields.

* The samples from the *Molinia* moor were taken from an area adjacent to a number of leys of different ages. This probably may explain the somewhat unlooked for occurrence of *Medicago lupulina* in this situation.

They were also recorded in nine out of the twenty-one arable fields. The populations on the lowland grass types increased from type 1 (first-grade ryegrass) to type 5 (*Agrostis-fescue*), dropped to nil in type 6 (*Juncus*) see Fig. 7. The upland populations on the average were considerably lower and those of downland slightly so.
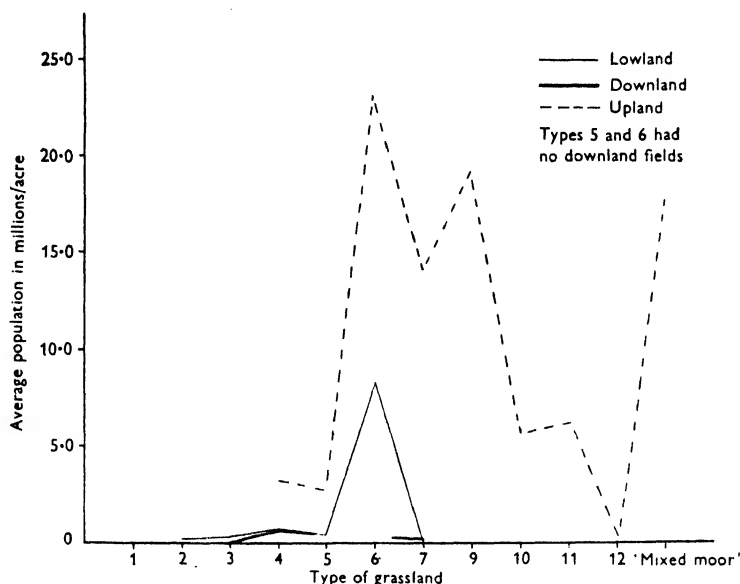
Fig. 7. *Juncus* spp.
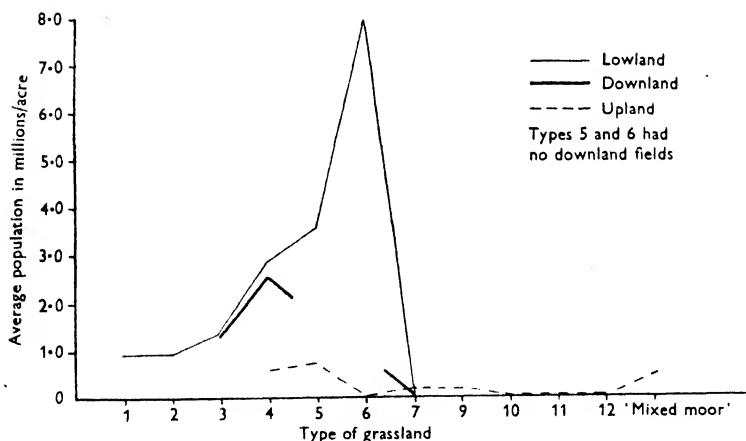
Fig. 8. *Ranunculus* spp.

The chief components of the populations were *Ranunculus bulbosus* and *R. repens*. *R. acris* was only a minor contributor with the exception of 1·26 million per acre on a type 4 upland field at Mixon Hay. *R. ficaria* was confined to the poorer habitats.

(*h*) *Sonchus.* The arable weeds of this genus are noteworthy for their consistent appearances on all grassland types; *Sonchus* (sow thistle) was recorded on all types except types 1, 12 and 'mixed-moor' (Fig. 9). The populations were generally, but not invariably, low and largely composed of *S. oleraceus*. The maximum population (11·75 million) was

recorded on a type 3 downland field: only one other field passed the million mark. *Sonchus* was recorded in twelve arable fields; here the maximum population of 2·88 million was recorded on a field representing type 3.

(*i*) *Other arable weeds.* Other typical arable weeds were not found in sufficient number to provide much evidence, but the following observations made during the course of the investigation may be of value. *Alchemilla arvensis* (parsley piert) appeared in samples from four arable fields—three lowland (one type 4, one derelict arable, one old arable now in ley) and one downland field (fescue). The maximum population was 1·5 million per acre. It was recorded in only two downland samples; both belonged to type 7 and the populations were low in both instances.

It is noteworthy that *A. arvensis*, *Medicago lupulina* and *Cerastium vulgatum* were all among the weeds studied by Brenchley & Warington (1936) in their work on arable soils at Rothamsted and Woburn Sands.
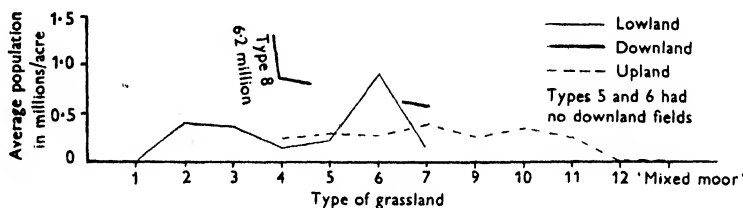
Fig. 9. *Sonchus* spp.

A remarkable feature in the present investigation is the comparative absence of *Papaver* seedlings—*rhoeas* has been the only species we have recorded. It occurred on a single field and there gave a population of 1·68 million seeds per acre. Other authors have found large quantities of buried *Papaver* seeds (Brenchley & Warington, 1930, 1933 and 1936). As far back as the eighteenth century large quantities of poppies were observed coming up in ploughed fields that had been under grass for many years (Lisle, 1757).

(*j*) *Calcicolous plants.* There are a number of calcicolous plants that were confined to the calcareous soils or to downland alone. The list includes plants such as *Poterium sanguisorba* (salad burnet), *Acinos arvensis* (basil thyme), *Blackstonia perfoliata* (yellow wort), *Campanula rotundifolia* (harebell) and *Fragaria vesca* (strawberry).

The pasture-arable bias shown by the species considered in this section suggests a qualitative as well as a quantitative difference in the seed populations of 'grass' and 'arable' soils—a difference often magnified in the 'arable' samples by the presence of large quantities of the seed of species that form the normal ingredients of herbage seeds mixtures.

D. *Results from the boxes kept into* 1946 (*second season*)

Germination was usually low in the five boxes retained for this further trial in the second germinating season (1946). One sample from Gloucestershire, contributed no seedlings at all in 1946 after having produced the equivalent of 14 million per acre in 1945. Another, from Cheshire, produced only five seedlings in the second year. Sixteen plants germinated in a sample from Wiltshire. This was equivalent to a population of 2·64 million per acre, approximately a fifth of the previous year's germination (12·51 million). This aggregate figure of 2·64 million was contributed to by eight different species.

Germination was much higher in the two remaining boxes. Thirty-three plants were removed from one sample. The twenty *Juncus bufonius* seedlings represented a *Juncus* population of 3·42 million against 7·19 million in 1945. The other box produced a total of fifty-nine seedlings, fifty-one of these were represented by *Coronopus squamatus* giving a population of 6·74 million per acre compared with the 1945 germination of 0·66 million.

The above evidence suggests that results based on the 1945 germination were substantially reliable for most species, but incomplete and possibly misleading in respect of a few species.

E. *Comparison of* 1940 *and* 1944 *results from the same fields*

The 1944 figures for the total populations of the fields at the Station are compared in Table 6 with the 1940 figures discussed by Milton (1943). The direct comparison is not absolute because the figures given by Milton represent 2 years' germination while the present data largely cover 1 year only. However, this error is probably small and at least in the agriculturally important species can largely be disregarded (see above, p. 166).

Table 6. *To show the* 1944 *buried viable seed populations for five fields at the Station compared with their* 1940 *records*

Year of sampling		Populations in millions per acre					
		Field 2	Field 12	Field 21		Field 25	Field 32
1940	Condition of field	Derelict arable	Derelict arable	Tor-grass		Tor-grass	Worn-out
	Viable seed population	55·28	42·79*	65·72		49·09	28·37
1944	Condition of field	Herbage for seed	Ley	Treated ley	Untreated tor-grass	After beans	Ley
	Viable seed population	86·91	20·45	47·77	40·49	8·27	9·57

* Average parts I and II.

Three of the Station fields under consideration (F 21, F 25 and F 32) were in grass when sampled in 1940, but these had been ploughed before 1944. F 21 was treated as one unit by Milton, but by 1944 only half the field had been ploughed so it was sampled in two sections in the latter year. Two of the fields, F 25 and F 32, showed a very marked reduction in the weed population. The population of the third (F 21) was reduced, but the reduction was greater on the part still down to grass than on the ploughed part. This appears to contradict the theory that cultivation reduces the number of viable seeds. However, the 'treated' portion contained several million seeds per acre, representing species normally used in seeds mixtures while the unploughed portion had approximately 50 % tor-grass (*Brachypodium pinnatum*), which contributed nothing to the buried seed population. Also *Agrostis* had a better chance on the treated part (*Agrostis* population 19 million), from which the tor-grass had been cleared. This may explain the apparent discrepancy.

The seed populations of the arable fields (F 2 and F 12) showed a variable response to improved cultivation, they were reduced on F 12 and increased on F 2. The latter increase can be attributed to 33 million seeds per acre of sown timothy. Seed crops of timothy and cocksfoot had been taken on F 2 in 1942/4.

DISCUSSION

Agriculturally the chief importance of this survey is that it gives an indication that the potential weed population following cultural operations is lower for some types of grassland than for others. This potential population is small on the best ryegrass pastures, high

on the poorer ryegrass, *Agrostis* and *Agrostis*-fescue fields and again low on the fescue types. It must be remembered, however, that the survey referred to seed populations only. No account was taken of large-scale regeneration from small vegetative pieces characteristic of plants such as *Allium vineale* (onion) and *Cirsium arvense* (field thistle). Also the number of fields examined of any one type varied from one to five. It would be necessary to repeat the investigation on a larger scale before definite conclusions could be reached or statistical analysis applied. The variations between samples of the same type were often large so that results from types represented by one field only cannot have much significance. It was to overcome this difficulty of one-sample types that tables for 'grouped' types were included where all figures represent an average of a number of fields. Had more samples been taken a number of the aberrant figures would probably have been 'ironed out'. Results representing the average figures for the fields of any one type would certainly have been more reliable.

One fact stands out: arable populations were consistently lower than those of their grassland counterparts. This suggests that a few years good cultivation will reduce the weed seed population. This was, however, only partially upheld in the comparison of the results from fields at the Grassland Improvement Station with the 1940 figures for the same fields. These findings do not agree with those of Brenchley (1918), who also compared the viable seed populations of fields under grass and arable. This worker found that the seeds of arable soils were more varied and occurred in greater numbers. On the other hand, Prince & Hodgdon (1946) working on the buried seeds beneath pastures found the viable seed population much lower in a recently tilled pasture than in one which had not been ploughed for 50 years. They concluded that the reduction might have been caused by germination and death of dormant seeds during the cultivation processes.

Milton (1936, 1939 and 1943) links the size of seed populations with the theory that seeds survive best under damp or acid conditions. It is interesting to examine these results in relation to the water content and the pH of the soils sampled. For example, the water-logged conditions of *Juncus* habitats are almost certainly the cause of the large seed populations found there. The increase in viable seed populations from first- to third-grade ryegrass and *Agrostis* pastures is possibly connected with an increase in acidity, but it is unlikely that this is the sole factor involved since the best pastures were probably under the most efficient system of management and were, therefore, allowed less opportunity to seed.

Soil conditions may be responsible in part for the low viable seed populations found in arable soils. Arable land is frequently more adequately limed than grassland and, therefore, has a higher pH. Further, the drainage of arable fields on heavy land often receives more attention than that of grassland fields in similar situations. Thus arable fields tend to contain less excess moisture and to be better aerated. There are, however, other differences between the habitats provided by grassland and arable fields. Not only does cultivation turn the soil bringing deeply buried seeds nearer the surface: it also introduces the light factor through the removal of the vegetative cover. The importance of light in the germination of buried seeds is suggested by Donald (1941).

It is interesting to consider some of the population:species ratios in relation to Milton's theory. The ratio is very high for *Juncus* types. The limited flora of these areas has caused the average contribution of each species to the sward to be high, but the high ratio is probably also closely connected with the characteristic environment of the *Juncus* types.

Water-logged soils tend to be cold, poorly aerated and sometimes acid. Such conditions appear to be good for seed preservation but to inhibit germination (Milton, 1936, 1943; Kidd, 1914). It is worth noting that the heavy germinations obtained from these were not *in situ* but took place in the greenhouse where the moisture, aeration and other factors of environment were artificially controlled. The large number of ryegrass seeds found in a sample from a *Juncus-Carex* association has been mentioned. In this connexion Milton (1939) says 'The soils underlying *Juncus* areas containing very few other species in the herbage were found to contain viable seeds of a more numerous flora'.

The high population:species ratio and the heavy *Calluna* viable seed population on the heather-moor are probably related to the good preservation of seeds in acid peats.

The ratio population:species of downland is low and may be correlated with the poor survival of seeds in soils of high pH and low moisture content. At least two factors, likely to inhibit germination in water-logged soils or acid peats, poor aeration and a high concentration of carbonic acid conditions are absent under downland. Thus the seed turnover would be expected to be much more rapid in downland than in acid or water-logged conditions. Soils of high basicity are probably unfavourable to seed preservation because many bacteria involved in the breakdown of organic material thrive under neutral or slightly alkaline conditions. This would also appear to be true of fungal attack; Turner (1933) mentions that this form of decay appears to be inhibited by the antiseptic properties of peat. A third factor may also be partly responsible for the low population:species ratio, the natural flora of the downland associations is large and characteristically varied, thus each species makes only a small contribution to the sward.

A different approach is to consider the populations of individual plants in relation to this theory. From this aspect even the *Lolium perenne* figures seem intelligible. Suppose *Lolium* seeds are potentially sensitive to environment and do not survive long except under acid or wet conditions. Could not the increase of ryegrass seeds with the decrease in the herbage be related to the greater acidity of both the poorer ryegrass and the *Agrostis* types? The extreme case of the excellent preservation of ryegrass seed in water-logged *Juncus* soils has been discussed already. This theory can also be successfully applied to populations of *Festuca* but still leaves the anomalies associated with the figures for *Agrostis*.

In any future buried seed experiments it is hoped to make an analysis for pH on each field when sampled. This will enable the thesis to be pursued further and provide results of immediate interest.

Milton (1943) mentioned the importance of high populations of legumes found on the calcareous soils at Stratford-on-Avon. His figures showed wide variations, but he recorded some very high populations of 10 million viable seeds per acre. Only one legume population of this order was recorded in the present survey (9·28 million). The calcareous soils under investigation did not contain a specially high proportion of legumes.

The comparison between the first- and second-year germination shows that the majority of seeds germinate in the first year. This agrees with Milton (1943) and Brenchley & Warington (1936). Brenchley & Warington show that germination of some species continues in reduced quantities for upwards of 10 years. The data obtained from the present survey, together with those of other workers, show that wherever possible such experiments should be continued for a minimum period of 2 years. The indications are such that a 2-year period would allow for the germination of the great bulk of the seed in

most species. Where trials of this nature are concerned only with problems of an immediate practical nature then even a 1-year period would suffice to cover the potential germination in most species of agricultural importance. Where, however, the problem of comparing widely contrasting species is under investigation then experiments dealing with viable seed populations should be conducted for at least three consecutive seasons. Further work is required to find whether or not such processes as freezing and other environmental changes (Nichols, 1934; Ministry of Agriculture, 1946) will induce more rapid germination when soil samples are returned to a more normal environment.

Clearly, from a purely practicable point of view, it would be wholly advantageous if it proved possible to induce germination throughout the range of species so that the samples collected in one year could be discontinued at the end of the following season. Better still, if the period of potential germination could be reduced to a matter of months we should then be able to provide the practical farmer with a method of determining weed and other seed populations which would be of immediate service to him in his year to year cultural treatment of arable and other fields.

The investigations at this Station in connexion with buried seeds are being continued, and it is to be hoped that data having practical as well as scientific interest will emerge. The present paper therefore is to be regarded in the light of a progress report which deals largely with the initial aspects of the work. The report describes the results of a widely flung survey of specific fields all over England. The survey has not been in any way complete, but it has gone far enough to show that the populations of buried viable seed in ordinary grassland fields can be very material and may amount to many million per acre.

It is of practical interest to discuss some of these maximum populations in terms of seed rate per acre, given that they would all germinate together in the soil. We know by the epidemic occurrence of many of our weeds after ploughing up pastures that quite frequently we do find very high germinations of such weeds as buttercup, daisy, geranium, rushes, thistles and in the grasses, especially *Agrostis*, fog and meadow grasses.

We have found a maximum population of 57 million viable seeds of *Agrostis* per acre— this represents a seeding of 12·8 lb. per acre. Table 7 shows a number of these high populations in terms of lb. of seed per acre.

Many of these quantities are of the same order as seed rates used in seed mixtures and it is easy to see how a ploughed field will rapidly regain a vegetative cover. It is interesting to correlate the large weights of the meadow grasses, *Poa trivialis* and *P. annua*, with a practical experiment carried out by Worthington (1947). This worker has obtained swards of almost pure meadow grasses for poultry by allowing the buried seeds to germinate and establish themselves after a period of cultivation during which time seedlings of a number of other species appeared and were destroyed.

The large quantities of buried viable seeds present in most soils are closely connected with two problems of ley farming—establishment and retrogression.

Weed competition is one of the factors the newly sown seeds mixture has to stand up against in the fight to establish itself. It is frequently a very serious menace and often requires active aggression on the part of the farmer to tip the balance in favour of the sown species.

A comparatively weed-free sward in the seeding year does not mean the battle is over, although the sward is more stable by its second year. Even a well-managed ley usually shows some increase in unsown species as the years go on, and retrogression may be

considerably hurried by mismanagement especially over-grazing followed by under-grazing. The sward may be considered to be in a state of unstable equilibrium and each plant in it is competing with its neighbours for light, air, space and moisture. If a plant should be weakened or pulled out during grazing its neighbours may encroach or the bare spot may be covered by the germination of one or more buried seeds. Should these establish themselves, they would provide a foothold from which the species concerned could take its place on the competitive ladder.

Table 7. *To show some high viable seed populations in terms of lb. of seed per acre*

Species	Weight per 1000 seeds (g.)	Viable seed population in millions per acre	Equivalent in lb. seed per acre (lb.)	Authority for weight
Grasses:				
Agrostis spp.	0·10	57·92	12·8	Milton
Dactylis glomerata	0·9	15·12	30·0	Jenkin
Festuca rubra	1·1	6·74	16·3	Jenkin
Lolium perenne	1·99	8·72	38·1	Jenkin
Poa annua	0·2	12·27	5·4	Salisbury
P. trivialis	0·25	0·25	32·0	*
LEGUMES:				
Lotus corniculatus	1·2	5·39	14·3	Salisbury
Trifolium dubium	0·3	14·38	9·5	Harshberger
T. repens	0·64	8·07	11·4	Jenkin
OTHER SPECIES:				
Bellis perennis	0·15	11·8	3·95	Salisbury
Calluna vulgaris	0·025	56·72	3·12	Authors
Carex spp.	0·61	3·4	4·57	Milton
Cerastium vulgatum	0·10	5·43	1·2	Milton
Juncus squarrosus	0·0275	18·77	1·1	Dallman
Plantago major	0·2	3·52	1·5	Salisbury
P. lanceolata	1·42	2·18	6·8	Salisbury
Potentilla reptans	1·8	4·17	16·5	N.I.A.B.
Poterium sanguisorba	8·89	2·79	54·7	Jenkin
Ranunculus repens	1·73	6·33	24·1	Milton
Sinapis arvensis	1·96	1·09	4·7	Salisbury
Sonchus arvensis	0·336	11·66	8·6	Salisbury
Stellaria media	0·505	5·07	5·7	Salisbury

* Calculated from figures quoted by Stapledon & Davies.

SUMMARY

1. Samples were taken from different types of grassland. Some fields were included that had been ploughed up since they were classified during the Grassland Survey of England and Wales. A number of samples came from the Grassland Improvement Station at Stratford-on-Avon and the Sub-Stations of Colesbourne and Mixon Hay.

2. Details of the sampling and greenhouse procedure are given. Germination took place over one season only.

3. The results show that the arable fields under investigation contained fewer buried viable seeds than the grassland fields. This indicates that cultivation reduces the weed seed population.

4. The results also showed a general increase in both the number of species and the populations of viable seeds from first-grade ryegrass to *Agrostis*-fescue pastures.

5. The ratio of viable seed populations:number of species was low on downland fields and very high on *Juncus* fields where the flora is more limited.

6. The moorland types gave irregular results. The number of viable seeds was greatly affected by the presence or absence of the few moorland plants that run to high populations, namely *Calluna* and *Juncus*.

7. The calcareous soils under investigation did not contain a particularly high proportion of legume seed.

8. The correlation between the sward and viable seeds buried beneath is shown to be incomplete. Evidence is given to support the conclusion that buried viable seeds of some species tend to be found in large numbers while those of others are scarce.

9. The data for the individual species are summarized and a few genera and species are considered in detail. The populations of some plants, such as *Ranunculus* spp., closely parallel their ecological distribution. Populations of others, including *Agrostis*, appear to bear little relationship to their contribution to the sward.

10. There is evidence of a broad correlation between the results of this survey and the theory that seeds preserve best under acid or water-logged soil conditions.

11. Evidence is also given that germination should be continued over a second season in future experiments.

12. The seed populations of the fields at the Grassland Improvement Station were compared with the earlier figures for the same fields. These results only partially upheld the view that cultivation reduces the viable seed populations.

13. Some of the high viable seed populations are shown in terms of lb. seed per acre. These quantities are of the same order as seeds sown in seeds mixtures. Reference is made to the relation of these populations to the problem of establishment and maintenance of a clean sward.

14. The number of samples of each type was small, consequently the conclusions reached must be considered as tentative. The results do, however, provide interesting pointers and additional information to verify the earlier findings.

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WHAT MEANS THIS DROUGHT?

By Professor ALWIN SEIFERT, *Munich*

A new plague has now joined wars and revolutions and atrocities which seem to mark our age: the great drought of 1947.

It is not in the last resort man-made. Such human mistakes as I dealt with, more than ten years ago, in my article on the 'steppification' of Germany (*Die Versteppung Deutschlands*) (the overdraining of the land for a century and more; the extirpation of hedgerows, tree-lines and copses; the undue exploitation of our forests, which has of late taken on pace and the character of a mere senseless destruction) contribute to accentuate the effects, but they do not account for the origin proper of the drought. These factors, even if remedied or undone as by a stroke of miracle, would by no means counterbalance what I consider to be a basic change of climate: a change from maritime to inland climate.

Degrees of heat unrecorded since the beginning of regular meteorological statistics were observed in Central Europe during last summer. In many districts no rain fell from the melting of the snow till late autumn. Though, in other districts, some months have brought rainfalls even above the average, the moisture was eaten up by hot and uncommonly dry winds before it could become available to vegetation. No water sank into the soil to replenish sub-soil water and springs. The effect of this dearth of water has continued right into the winter. And so will the failure of crops continue into this year's harvest wherever the winter-seed could not be brought under the surface or refused to germinate in the dry soil; wherever fertilizing elements in the soil have disappeared under the merciless sun of last summer; wherever so many cattle had to be slaughtered that natural manure for the fields is lacking.

The mention of these effects suffices already to bring home that the rows of figures collected by meteorologists in their tables do not tell us overmuch as to the influence of these collected data on plant-life. To meteorologists it was a summer uncommonly warm and poor in precipitation. It remains for the farmer, the forester, the peasant to say that it was a drought: they are up against 'climate' as an organic, effective entity, where meteorologists observe and record detached symptoms only.

A glance back over weather conditions in the last decades will show that the dry year 1947 was not a single, accidental event, but one among a considerable number. The years 1911, 1921 and 1929 were hot and dry, but there was no failure of crops. Wine connoisseurs think back to those vintages with shining eyes. The year 1933 was hot and dry, yet we had a record harvest; 1934 and 1935 were similar; while 1937 was another excellent wine-year and we had a record harvest like 1933 (though it cost us the fourfold of artificial manure). The years 1942, 1943 and 1944 were also dry and warm in summer, but 1945 is fresh in our memory as one of the longest and finest summers. The spring of 1946 was completely dry for many months, yet some few timely summer rains brought on a tolerable harvest. Only bee-keepers called it a year of drought, because the moisture did not reach far enough down into the ground to find the roots of the plants that provide summer-pasture for bees.

It is this frequency of hot and dry summers which seems more remarkable than their individual records; though certainly 1947 seems to have formed a climax also in absolute records.

Moreover, into this series of summers are inserted, with equally uncommon frequency, cold and coldest winters—1928/9, 1939/40 and 1941/2—which latter cost Germany nine-tenths of her plum trees and the half of her apple and pear trees and, incidentally, materially helped to turn the tide of war in Russia. Further, 1942/3 and, in the end, that cruel and long winter 1946/7, which, in Northern Germany, will go down in the memory of men as a Scourge of God.

Into this accumulation of hot summers and cold winters there falls, curiously, in early summer 1940, the highest of all recorded floods, at least for the northern foreland of the Alps. A veritable catastrophe of subsoil water pressure followed it, causing the large gravel-pit lakes along the newly built motor-tracks north of Munich to overflow and putting the technical plant in the cellars of our airport out of action for years.

Extremes of heat and cold, of dryness and sudden torrential rains characterize an inland climate, whereas Germany had hitherto been within the reach of a maritime climate with moderately cold winters rich in precipitation, and moderately warm and damp summers with steady and even rains instead of quick thunderstorm downpours.

In 1936 I wrote, in an article which caused some discussion in Germany: 'The climate of central Europe seems to swing back, after four centuries of greater moisture, to a degree of dryness comparable to that obtaining in the Middle Ages.' (*Die Versteppung Deutschlands*, 1936.)

A leading meteorologist then rebuked me severely because of my 'unfounded assertion'. I had come to this conclusion from an intimate observation of small facts in Nature, separate and correlated at the same time, which seemed to me to point to something radically different from the usual ups and downs of meteorological data. This more radical change of climate seemed to coincide with other, perhaps still more fundamental changes, which I had, in another article (1934), outlined as follows: 'In our days comes to an end that period which history-books call the Modern Age. The world is in a fever of unrest as it never was since the beginning of this period, since the days of discoveries and inventions, of Reformation and social unrest. There is a revolution of all certainties and values.'

Can a connexion, of whatever nature—certainly it will not be a straightforward 'causal' connexion in any mechanistic sense—be shown between changes of climate and political, social and cultural revolution? I think, in fact, such a coincidence does suggest itself for periods which go to make the heritage that now seems to crumble under our uncertain hands: the European Middle Ages, the Modern Age from 1500 onward, and even that longer period which some call the Period of the Fishes and others the Age of Christian-occidental civilization. The rise of all of these was heralded or accompanied by a change of climate in Europe.

After the end of the glacial periods the climate had, in ups and downs, gone on improving, making for that long period of warmth during the Bronze Age which was perhaps the happiest period of our old Europe, the *juventus mundi*. In the Alps, the glaciers had almost all vanished. Valleys facing south became so dry that settlers had to drive their cattle, over the high and dry Alpine passes, to the cooler and moister valleys facing north. Since that period of 3000 years ago, thousands of cattle and sheep wander, down to our own days, to and fro in summer over Austrian and Swiss Alpine passes long

covered again by ice and snow. Thus firmly this Bronze-age necessity still governs to-day's usage, economy and local laws.

This Bronze-age climate drew to an end during the last centuries before the birth of Christ; a period marked, in its human aspect, by the disintegration of classical antiquity properly so called, a very real Period of Transition, to be gathered up, for a time, in the short Indian summer of the Augustan Age.

During those centuries our climate turned. The Alpine glaciers spread, the shafts of the salt-mines in the Alps became submerged, preserving for us in newly formed crystallizations the tools of the older age, and in folk-stories haunting their localities the tales of the 'Man in the Salt'. Mineral mining in the Tauern range ceased. Also north of the Alps it became cold and unfriendly. The open groves of oaks with their glades and undergrowth of hazels turned into the dense, gloomy, boggy and foggy forests of 'Germania', which a little later the Romans came to know and to abhor. Crop failures and general inclemency of life started that century-long predatory and land-taking migration of Celtic and Germanic tribes towards the south. Italy, Spain, the Balkans, Greece and even Asia Minor were invaded in turn.

Not until the growth of the Holy Roman Empire, in the twelfth and thirteenth centuries, did Cis-Alpine Central Europe blossom again into full warm summers. This was one of the reasons for the colourful splendour, the power and optimism of our medieval Empire. In the Alps the glaciers receded far enough to allow gold-mining to be taken up again in the Tauern range. The vine spread from its Roman home along the Rhine over the whole extent of country between the Alps and the Baltic Sea. Vine-yard, vine-field, vine-garden, vine-slope are still to be met with all over the place, as ancient field-names (*Flurnamen*), even in high and now quite inclement mountain-valleys. The Teutonic knights, up in their castles along the Vistula and the Baltic, welcomed their guests with draughts from their own vineyards. Nor was it the tart 'throat-scratcher' or the sour 'cat-piss' later to be associated with the viniculture of the 'Diaspora'. A Bavarian duke reports of this Baltic wine in 1363 that it was 'a noble draught, sweet and heavy to make your mug stick'. In 1379 the Master of the Teutonic Order drew from his Baltic vineyards 30,000 (wine-) gallons of this wine.

This glory passed away with the decline of the fifteenth century, with the birth of the Modern Age—again a memorable epoch without and within: the physical world widening with geographical discoveries; the political world shaping into the Great Powers of later European history; the world of the mind widened by new concepts of personal and religious freedom, of moral freedom, through the Reformation; and the intellect enfranchising itself from the former metaphysical unity, eager to conquer the world of matter and soon to discover the fateful 'Knowledge is Power'.

Here, then, again a change of climate. The friendly vine withdraws to its old Roman home, the banks of the Rhine and its tributaries. It leaves some few languishing relics in Saxony (Dresden), in Silesia (Grünberg) and Bavaria (Ratisbon). Meteorologists, always loth to admit anything that is not in their tables, held up against me that this undeniable cessation of viniculture arose from the fact that roads grew better about that time, so that wine could be brought from afar more cheaply than it could be produced on the spot, where anyway its cultivation, according to them, had only been fostered so as to have a secure supply of wine for holy mass. This argument, however, does not seem to me to hold water. That along the Vistula viniculture was destroyed in the

fifteenth century by cold winters we know from chronicles. Besides, Rhenish wine was mostly exported in ships' bottoms and not on the axle, and the Teutonic Knights and the Hansa Towns on the Baltic would always have had enough money, ships and command of the sea to use that means during the Middle Ages. And on no account can wine, carted on the axle over 700 miles, even on improved roads, come cheaper than wine grown before your door which had not to pass through many toll-greedy little territories. That is, if you can get the grapes to ripen enough for wine. That was the trouble. The grapes no longer ripened after about 1500, except in their old home in the west.

There are other signs pointing to a change of climate about 1500. Locust plagues, frequently recorded in the warm Middle Ages, cease troubling Central Europe after 1500, though the devastation of the Thirty Years War (1618–48) which reduced the population of Germany to a quarter (from 28 to 6–7 millions), depopulating wide stretches of land, would have given them a good enough chance. Then there is a change in the use of building-timber. In the castle of Schattenburg in Vorarlberg, for example, I found the ceiling of the great Gothic hall constructed of stout beams of real sweet chestnut. Medieval cellar-ceilings in peasant-houses thereabout are of the same material. To-day, only two weakling specimens of this noble tree grow on the side of the Pfänder mountain above Bregenz. Nothing else is left to indicate that the Vorarlberg region was once rich in these trees.

After 1500, the Alpine glaciers advanced again. The miners put up a desperate struggle against the ice overrunning their pitheads dug into the mountain sides of the Tauern range. In vain. Mining for gold ceased there; the miners emigrated. The glaciers continued to advance, reaching their greatest extent in 1859. Woodcuts and steel-engravings of that time from Switzerland show many a glacier reaching down into the valley, where to-day only the topmost silhouetted line shows a fringe of glacial ice. Since 1860, however, the glaciers have receded rapidly; the years may be wet or dry, hot or cold: the glaciers recede. Meteorologists find no explanation for this retreat in their tables. In the last years, pitheads overrun by glacial ice after 1500 have appeared again in the Tauern range; one could restart working the medieval mines; the glaciers have, within the last 80 years, dwindled to their medieval dimensions. In Carinthia (Kärnten, south-eastern Austria) the summer climate has within the last 80 years taken on an unmistakably Mediterranean aspect. Precipitation has tended more and more to be localized at the beginning and the end of the season. Though the yearly averages in precipitation and warmth remained unaltered, the summer properly speaking became so dry and warm that mountain-pastures (Almen) facing south dried up.

Nature has, in her plants and animals, more sensitive indicators of climatic change than the meteorologists in their temperature and rain gauges. Science, for purposes of observation, must needs split up the integral of climate into differentiated quantities. Nature and things that are of nature register the whole. Since the eighties, eastern and south-eastern steppe flora migrates to the north-west. Southern locusts, butterflies, wild-bees and even mammals follow them. Goethe in his time had not known the hamster (*Cricetus* Pall.). It came in later from the East. The hamster abhors damp.

Such indications of growing warmth and dryness are not confined to Central Europe. The Sahara spreads southward a mile per year. The Caspian and Aral seas and lake Tchad are falling in level continuously. East and South Africa show signs of desiccation; South America and Australia have spells of drought increasing in frequency. Forests in

Southern Siberia dry up and perish. Glaciers in Iceland and Spitzbergen melt off; the Arctic waters have become appreciably warmer within the last years. The Mediterranean regions know crop-failures from drought much more frequently than formerly. In 1946 Sardinia and Central Italy had locust plagues as pernicious as ever in medieval times. From all over the earth we hear of desiccation; but nobody complains about getting too much moisture.

The thought suggests itself that great civilizations of the past have died off from a desiccation of their living-space. So again to-day any and every measure which furthers desiccation—like the terrible ravaging of forests at present perpetrated in Germany—is a crime against European civilization.

Seen in this light the great drought of 1947 loses its accidental, one-time character and ranges itself into sequences which point to a general change of climate in Europe and perhaps beyond. The speed has gained momentum of late, perhaps 1947 was already the climax. Can we do nothing but fear it? Twice before, we have seen, this sort of warmer climate has accompanied, if not brought forth, most genial periods in European history. Nature seems to offer our own new age a kindly hand. What must we do to grasp it?

We must be careful of the water-economy of Nature. Instead of draining water away as quickly as possible we must leave it where it was meant to be. At least as long as we are not sure how we can establish a new balance, acceptable to Nature, wherever we have thought fit to disturb her own balance for human profit. To this effect we must:

(1) Re-stock our tree- and bush-depleted countryside with the hedgerows, tree-lines and copses which figure so largely and beautifully in our medieval woodcuts and paintings. They retain moisture not only in the ground, but, functioning as it were as wind-breaks, they also retain moisture in that layer of air immediately above the earth which largely constitutes the micro-climate of vegetation. The plain of the River Po may serve as a present-day example.

(2) Preserve all ponds still extant and lay out new ones, as in the Middle Ages, when every monastic or peasant economy had its ponds.

(3) Cease straightening and 'cleaning up' all water-courses coming to hand. We must no longer, between concrete banks and similar ungodly devices, rush the water away, unused, from where it fell. We must no longer pass on all so-called floods to the fellow farther down, increasing *his* danger and forcing him to do likewise, until the water is spat out into the far Ocean where nothing grows.

(4) Study carefully and patiently—since we have lost the intuition—the whole complex of subsoil water, its levels, fluxes and reservoirs. We must no longer, in order to gain some square miles of agricultural land by draining a bog or a fen, unbalance the subsoil water economy for perhaps many square miles all round without heeding or even knowing what we are doing.

(5) Reafforest our large forests as quickly as Nature allows. For years past they have been drawn on unduly under the necessities of rearmament and war. But of late they have been ravaged in a most vile, unbusiness- and unforestry-like manner, by introducing the method of total mechanical razing, which to my mind is like fishing with hand-grenades. This method may have its merits in far-off, uninhabited, virgin lands, for large-scale clearances to stay. As a method of 'gaining' wood, and in the circumstances of Central Europe, it is nothing but downright pernicious and paving the way for Anarchy. It will be a matter of decades to reafforest.

Then, but only then, the grave warning of the great drought of 1947 may prove a blessing in disguise. Then the cultivation of maize may spread in Central Europe. Barley may take the place of too much oats. Perhaps even the soya bean may come to thrive. The old millet may reappear, which was, as 'millet-gruel' the 'bread' of our oldest fairy-tales. Millet-seeds brought some years ago from the Hindu-Kush promise well. They give a better return on dry soil than oats on moist soil.

Nobody can say that these perspectives are uninviting. Wines grown in Saxony, near Dresden, have improved from year to year and have, according to connoisseurs, of late again reached the quality of good Palatinate wines, as in the Middle Ages. In northern Tyrol, on a heap of debris which a wrongheaded road-construction had thrown down the mountainside, new vineyards were planted, and they give a fine return like those of the thirteenth century.

The late 'Modern Age' of history-books has left us stranded. Let us put our hands to the plough for our very own New Age. Nature seems not averse, if we heed in our dealings with her the maxims of two great men who, however different and even antithetical their views on the nature of Nature may be, curiously and significantly concur in this: I mean Francis Bacon's 'Natura non vincitur nisi parendo'—('you cannot get Nature to follow you except along her own lines') and Goethe's 'Nature will not be bullied, imposed upon or dallied with. She is always in the right, and the mistakes and faults are always man's'.

POSTSCRIPT TO 'THE EARLY HISTORY OF MODERN PLANT-ECOLOGY IN BRITAIN'

Some mention should have been made in this article (*J. Ecol.* **35**, 130–7) of C. B. Crampton's striking contributions to 'dynamic ecology'. Crampton was a geologist by profession, a member of H.M. Geological Survey, and he was attracted to the study of vegetation by the close connexion he observed between the plants and the geodynamic features of the Scottish mountain regions he surveyed. His papers on 'The vegetation of Caithness considered in relation to the geology' (1911), on 'The plant ecology of Ben Armine' (1912), and on 'The geological relations of stable and migratory plant formations' (*Scot. Bot. Rev.* 1912) showed a remarkable insight into the detailed relations between the small plant communities and the dynamic factors of unstable mountain habitats. His approach to vegetation had much in common with that of H. C. Cowles, of whose previous work Crampton was quite ignorant, and who was also trained as a geologist; and he attacked a side of field ecology too much neglected by the other British workers in the subject. Crampton's scientific career was tragically cut short in 1913 by serious mental trouble, and he died not very long afterwards.   A. G. TANSLEY.

REVIEWS

THE PECULIARITIES OF SOUTH AUSTRALIAN VEGETATION

Crocker, R. L. and **Wood, J. G. (1947).** 'Some historical influences on the development of South Australian vegetation communities and their bearing on concepts and classification in ecology.' *Trans. Roy. Soc. S. Aust.* **71** (1), 91–136.

This important paper describes and analyses the geological history of South Australia since the Cretaceous and then considers the effects of the more recent geological, physiographic and climatic changes in producing the existing soils, flora and vegetation. The results of the authors' studies have led them to the conclusion that existing concepts currently used in America and Britain for the analysis and classification of vegetation are inapplicable to South Australian conditions, and they suggest fresh concepts which they have found practically valuable. On analysis, however, there does not appear to be so much difference between them as the authors suppose.

The foundation of the later geological character of the continent was the general peneplanation which occurred between the late Cretaceous and the Miocene. In later Tertiary times there were considerable marine transgressions in certain southern areas, followed by recession of the sea approximately to the present coast line, and then by earth movements which, in South Australia, resulted in the uplift of the N.–S. running Mount Lofty-Flinders ranges in the south-eastern portion of the State, an uplift that has played a considerable part in the distribution of the existing flora. In south-western Australia much of the old peneplain is still preserved.

The Pleistocene period showed very different conditions from those of the northern hemisphere. The evidence is that there was adequate or abundant rainfall and damp atmosphere throughout, with fluctuating temperatures but no major ice fields in the continent. The dominating factor in the initiation of the modern vegetation was the occurrence of a period of extreme dryness which is tentatively dated at 4000–2000 B.C. The onset of this period of maximum aridity was very rapid. It destroyed a large part of the Pleistocene vegetation, and provided conditions for the formation of the very extensive series of continental sand dunes which cover so much of South Australia, the Northern Territories and Western Australia. Widespread wind erosion and the consequent formation of aeolian deposits and dune systems began so suddenly and was so extensive that the vegetation had no chance of maintaining soil stability, and an early replacement of the mesic flora by xeromorphic vegetation was not possible. Remnants of the pre-arid flora, nevertheless, survived these devastating conditions, migrating to the limited major hill ranges and their neighbourhoods. These 'refuges' were mainly the N.–S. Mount Lofty-Flinders range in the south-east of South Australia with some adjacent smaller areas, the E.–W. running Deering and Musgrave ranges on the northern boundary and the MacDonnell and James ranges in the south of the Northern Territories.

'The numerous ecological niches which acted as centres of survival were also the focal points from which began the migrations leading to the establishment of the present-day communities.' 'In all likelihood the isolation and continued stress of existence under conditions approaching the limits of tolerance of most species favoured a large number of sub-species and strains relatively unimportant previously, and resulted in endemism of varying degrees.' Subsequent increased rainfall and slightly lower temperatures would result in some release of the pressure of adverse climate and of competition. Migration would occur in many directions from the refuges, but since successful migration depends on the occurrence of 'a continuity of habitats which are within the ecological amplitude of the migrating species' (Cain), 'the main migratory routes in the development of the present South Australian flora have been from the survival centres along series of closely related soils.' These routes, with the soils they followed, are indicated in a diagram (fig. 6). 'As the migrations received their greatest impetus from a small increase of rainfall it is obvious that they proceeded progressively from more humid to drier areas.'

While the distribution of particular communities within any climatic zone depends upon edaphic factors, other things being equal, there are many striking cases of 'disjunction' in the distribution of species which are confined to areas separated by more than the normal dispersal capacity of the type. An example is *Acacia peuce*, a spectacular tree about 50 ft. high, which occurs as two small groups, each

of a few hundred trees, separated by 200 miles, though 'there appear to be ample unoccupied habitats within the edapho-climatic amplitude of the species'. It is thought to be a true relict, formerly widespread but restricted to ecological niches in widely separated localities as a result of the onset of aridity. *Eucalyptus cladocalyx*, the sugar gum, occurs in three localities, 100–200 miles apart, in one of which it is particularly depauperate and is thought to be near the limit of its climatic-edaphic range. The three populations are believed to have developed from three different centres of survival and to be true relict communities. Since the tree is much planted and evidently has a wide edaphic range it seems likely to have a poor migration (or establishment) capacity. Long-distance dispersal seems very improbable in such cases, though doubtless it is the explanation of distant isolated occurrences in the case of plants with very small and light propagules such as the spores of mosses and lichens, especially where the species can only grow in extreme specific habitats where competition is at a minimum. Thus *Sphagnum* occurs in two or three small swamps in South Australia, with the nearest recorded occurrence 250 miles away near Melbourne. The species is not mentioned—presumably it is the same. A somewhat different case is that of the two acacias, *Acacia sowdenii* and *A. loderi*, the former occurring in a fairly large area at the north of the Eyre peninsula in South Australia, the latter in the same climatic zone and on a very similar soil type about 150 miles away on the New South Wales border. The two species dominate communities containing a large number of the same associated species. These two acacias are very closely related, differing only in minor morphological characters. Clearly they are 'vicarious' species and in the authors' view are both descended from the same parent species, once widespread, and are the products of bio-typical isolation within that species, each having spread from a separate refuge. If this view is correct the two are *both* 'relicts' and *also* 'young' species in the sense of Willis's 'Age and Area'.

These cases make it clear that the historical factor is of decisive importance in explaining the present distribution of many South Australian species. The historical change which caused severe contraction in the area of a species may, nevertheless, have allowed the preservation of strain characteristics that allowed rapid expansion in the new edapho-climatic conditions when the restrictive pressure was removed. 'Young' endemics would also have become widespread if their ecological ranges were wide enough to permit dispersal and establishment either at a high level of competition, or, if they had developed prior to, or upon, the release of climatic pressure, at a lower level of competition. It would seem that some of the closely related pairs of species in the eucalypt sclerophyll forests may have had a similar origin. In the pluvial pre-arid period a series of suitable edapho-climatic habitats may well have existed to bridge the area now intervening between them. Isolation resulted from the aridity and has given rise to differential biotype selection. Besides the results of geographical isolation acting in this way reproductive isolation may be the result of extensive intercrossing and new segregations following the reunion of adaptive complexes developed under geographical or ecological isolation. Hence considerable differential speciation has probably occurred since the flora was broken up and isolated in numerous centres of survival during the desiccation. Though the progress of speciation has been limited by the relatively short time involved (probably 4000–6000, and at the very most 10,000 years) the normal rates of differentiation were probably greatly exceeded during the rapid expansion of the flora following the release of climatic pressure and before the brake of competition was applied by the attainment of something approaching equilibrium in the modern plant communities.

These considerations go far to explain many of the peculiarities of the South Australian flora and vegetation—the great complexity of some groups of species, the taxonomically 'good' species, not *genetically* isolated, which have been preserved during isolation by geographical or ecological barriers and have a great capacity for hybridization on reunion of groups, and the consequent great difficulty of classifying related species. It has recently been shown that the great polymorphism of the eucalypts is likely to have been produced in this way.

There are obviously large relict elements in the flora and many of the restricted species are old and not new endemics. The destruction of the pre-arid flora frequently meant extinction in one area and preservation in another nearby. But the modern plant communities themselves are young—i.e. the combinations are new.

The authors have not found it possible to apply the general theory of succession to climatic climaxes to South Australian vegetation, and they suggest that this is due to its origin by the re-colonization of vast bare areas by dispersal from centres of survival. The 'associations' are very young and 'their distribution has been determined within a climatic zone chiefly by edaphic conditions. The distribution patterns have

been greatly influenced, however, by other factors, such as individual dispersal capacities, chance dispersals, opposing migrations, location of survival centres, biotypical differentiation barriers, etc.' It is not surprising that the final species-aggregates are not made up of units with identical tolerances. 'In the Tertiary, when Australia was reduced to an almost perfect peneplain, climatic climaxes would perhaps have been recognizable in the theoretical sense.'

The authors accordingly conclude that 'succession should not be used in any scheme of classification'— a negative conclusion that may very well be valid in regard to the vegetation with which they had to deal, where allogenic factors are the important determinants, but cannot be applied to the regular autogenic seres which are clearly demonstrable in other parts of the world. The typical prisere is autogenic, not allogenic, in essence, though allogenic factors may also be involved.

The units they prefer to use are defined as follows. An *association* is 'a constant association of dominant species recurring in similar habitats', dominant species referring to the dominants of all the layers of a forest community. 'This is the grouping of greatest use in vegetation studies in Australia, though not necessarily the most fundamental unit.' Smaller units are the *type* (borrowed from the practice of foresters) and the *society*. *Type* is 'a local change in the dominants of the upper stratum of an association which is accompanied by little or no change in the other dominants'. 'A *society* is a local change in the dominants of the lower stratum.' The 'society' as here defined is practically the same as Clements's 'society'. The present reviewer's definition would include the authors' 'type', since it would refer to any 'local dominance' of species other than the typical dominants of the association; but in such a use the association cannot be completely composed of 'types' or 'societies' as it apparently is in the authors' conception, since the main part of the association is characterized by the typical dominants. Clearly there is some confusion here.

The authors criticize, not without some justification, the reviewer's recognition of the oak-beech (climatic climax) association of the European deciduous forest formation. It is based, of course, on the fact that *Quercus robur* and *Fagus silvatica* are the leading climax dominants of the deciduous forest from Poland to the Atlantic coast and are not uncommonly associated, though more usually they segregate into distinct consociations, while the oak stretches right across European Russia to the Urals. Furthermore, they are *commonly* accompanied by many of the same shrubs—for example, hazel—and many of the same field layer species throughout the area. This far-ranging 'association' shows great variation in subordinate species in different parts of its geographical range and on different soil types; and it is perfectly true that there are different consociations, both of oak and beech, on extreme types of soil, which have no species in common with one another. As to the criterion of 'constant habitat' this can only refer, in the case of a 'climatic climax' association characterized by specific dominants, to the climatic factors which determine the occurrence of those dominants with their associated species on a wide range of soils, and must neglect the other factors of particular habitats within the area. It may well be contended that such an 'association' is too large and 'ragged' a unit to be given the same category-name as more sharply defined associations which are generally recognized.

A fourth term used by the authors is *edaphic complex*. This is defined as a group of 'associations on nearly related soil types and with related floristic composition', within definite climatic limits. An example is the group of associations found on podsolized soils in the Mount Lofty ranges within the climatic zone limited by the 25 and 50″ isohyets. These are dominated by five species of *Eucalyptus* and have mostly the same associated species throughout, though with different frequencies, constant for any one community dominated by a particular eucalypt. They are developed on a considerable range of podsols of different types, varying in their nutrient and water relations.

With regard to the terms used by the authors for different categories of community there is really little difference with the slight exceptions noted, from their applications in Britain and America. The word 'type', however, is unsuitable for application to a particular category of community, in spite of its employment by foresters. It is always undesirable to attempt to 'technify' a word which has the widest general significance in ordinary language. 'Type of vegetation' will inevitably continue to be used in a purely general sense. The authors' contention that a seral system of classification cannot be applied to a vegetation developed under the special conditions of South Australia may very well be true, but that is no argument against its use in regions where progressions to various kinds of climax are clearly demonstrable.

A. G. TANSLEY

Trapnell, C. G., Martin, J. D. and Allen, W. *A Vegetation-soil Map of Northern Rhodesia.* With accompanying memorandum by C. G. TRAPNELL. Pp. 20, two 34-tone maps. 1947. Lusaka: Government Printer.

Detailed reports of the ecological survey in Northern Rhodesia have appeared in previous government publications (1937, 1941 and 1943), and it may be said that the pioneer work is rounded off by the presentation of this vegetation-soil map and memorandum.

The map is on a scale of 1 : 1,000,000 and is to be used in conjunction with the topographical map of the same scale. It is primarily a vegetation map with supplementary indications of the types of soil occupied by each type of vegetation and has been composed from a number of field traverses with additional information from aerial photographs and travellers' records. The complex pattern of vegetation and soil types has been successfully indicated by the use of thirty-four tones derived from three primary colours with letters superimposed to simplify reference to the chief soil groups. The printing and lettering is clear, although the colour tones are slightly variable in parts.

The memorandum gives a brief summary of the types. The classification of the vegetation is based on seven principal groups of which mention may be made of the evergreen and deciduous woodlands, the grasslands, and the intermediate savannah types of high grass and woodland, and grass with bush clumps or scattered trees. As with comparable types of vegetation in East and South Africa the most conspicuous and abundant trees are the deciduous Leguminosae. In fact, of the twenty-six genera used to typify the bush and woodland vegetation fifteen belong to this family and some, like *Brachystegia, Isoberlinia* and *Acacia*, are represented by several species. There is a far better distinction of the bush and woodland types than of the grassland types which are dealt with rather arbitrarily on a physiographic basis.

The profiles and other field characters of the soils of eight principal types and some subtypes are given. There is a tendency with tropical temperatures and low rainfall towards the accumulation of lime, but with increasing rainfall red earths and lateritic soils are found. In more temperate regions of high rainfall podsolic types develop. The affinities of the various soils are set out in the form of a diagram which, although it tends towards over-simplification, does clarify the general classification put forward.

One of the most welcome features of the memorandum is that references are given to the soils of East Africa, as described by Milne, and to those of South Africa, as described by van der Merwe, and wherever possible similarities or affinities have been noted and in some cases the nomenclature has been adopted. In this way it is possible to link up the soil-vegetation types in different parts of the continent. For example, the Kalahari sands make a deep extension into the western part of the territory, and the plateau soils, with many variations of the *Brachystegia-Isoberlinia* complex, form one of the most extensive types which corresponds to a similar type in East Africa and can be compared with the ferruginous lateritic soils of the northern Transvaal, where the deciduous woodland is of somewhat similar composition.

From the large amount of material at his disposal the author of the memorandum considers that on the whole there is a good correlation between the soil and vegetation types. This conclusion is well borne out by the map, probably because the simplification necessary in producing it directs attention to the general vegetation-soil complexes while minor differences have had to be omitted, so that the association of a single soil type with a vegetation type is fairly consistent and in most cases variations of vegetation and soil occur concurrently.

The final section of the memorandum is on land usage and summarizes the foregoing information, using the vegetation as an indicator for the potential agricultural and forestry value of the soil, in so far as land usage up to the present has shown what these soils will produce.

The memorandum is concise and well put together, and besides fulfilling its purpose as a key to the vegetation-soil map, it is a good introduction to the more detailed reports and serves to emphasize the thoroughness and efficiency with which the pioneer work on ecological survey in Northern Rhodesia has been carried out.

E. E. A. ARCHIBALD

Colvin, Brenda. *Land and Landscape.* Pp. 258, 106 photogravure illustrations and 17 text-figures. 21*s*. net. John Murray.

The ecologist will find this an interesting book though one which may well sadden him. It is a well-written and readable account of the principles of landscape design and control in Britain and, in short, it principally envisages the wider development of man-made landscapes. This is a natural and inevitable development of the age in which we live and of our overcrowded island. Thus long views are becoming increasingly important and their general character needs to be envisaged.

The book surveys three main groups of topics. First comes the historical background of British landscape. Secondly, the elements of design are discussed, the importance of land-use, of topography and of ecological background being adequately discussed. This section includes discussions of the role of form and colour, and of the types of plant material and their groupings. Finally comes a division of the field into the landscape types, urban, industrial and agricultural and the measure in which these may be treated.

The treatment of these subjects is sympathetic and intelligent and the whole is illustrated by a large number of half-tone illustrations of good quality. This is a book worth buying, for those who have an interest in this field. W. H. P.

PAPERS OF ECOLOGICAL INTEREST RECEIVED

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BRITISH ECOLOGICAL SOCIETY

SUMMER MEETING AT BANGOR

17–21 JULY 1947

Only about thirteen outside members were able to attend owing to the short notice of the Meeting and the fact that it clashed with an important Botanical Exchange Club excursion to the Scottish Highlands. However, those who were present made up for their lack of numbers by their keenness. It was nice to see the younger members of the Society taking advantage of these meetings. The party was very comfortable at the Bala-Bangor Hostel of the University.

The meeting started with a soirée on the evening of 17 July at 8 p.m. at the Botanical Department. Prof. Thoday welcomed the Society on behalf of the College authorities and recalled the previous visit to Bangor many years before. He also announced several minor changes in the programme issued to members, due to difficulties of transport. A number of exhibits had been put up by members of the staffs of the Departments of Botany and Agricultural Botany, including 'Contractile roots in *Oxalis* species' (Miss A. J. Davey), 'Draft map of vegetation and distribution of human settlement in the Conway Valley' (Dr R. E. Hughes), 'Distribution of fresh-water algae', 'Interesting local plants', 'Vegetation maps of South Snowdon' (Dr N. Woodhead). Refreshments were served and a very pleasant evening terminated about 10.30 p.m.

Friday, 18 *July*

After travelling by omnibus to Conway the party first visited Bennarth woods, by kind permission of Sir Joseph Kay. This excursion was led by Dr R. Elfyn Hughes. Bennarth woods from documentary evidence were woodlands in the early eighteenth century, when tree felling was recorded there, suggesting earlier establishment. Over a major part of the wood planting has been extensive, but marginal to the Conway estuary, it appears that some of the native characters of the wood have been partly preserved. The parent materials of the soils were Silurian shales and grits; glacial drift was absent. A soil profile was exposed which showed a well-developed A_0-horizon (3–4 in.) of dark raw humus. This passed to a rusty brown light loam; no evidence was seen of a distinct A_1-horizon. The profile was interpreted as being either weakly podsolized or a secondary podsol developing following earlier erosion.

Quercus petraea characterized the tree layer with some inter-planted beech and conifers. The ground flora was dominated by *Luzula sylvatica*, its chief associates being *Deschampsia flexuosa*, and local societies of *Pteridium aquilinum*, *Vaccinium myrtillus*, and *Calluna vulgaris*.

Coetmor wood which lies a mile to the west of Conway was next visited. The parent material of the soil was a colluvium of rhyolite (Ordovician) in relation to which a distinctly podsolic soil had developed, a well-marked podsol profile being exposed. In one instance, the B-horizon could not be reached on account of its depth and the boulderiness of the site. As in the first wood, *Quercus petraea* was the tree dominant accompanied by much *Betula pubescens* and *Sorbus aucuparia*. *Ilex aquifolium* was abundant in the shrub layer, with some *Corylus avellana*. The ground flora was rather sparse, dominated by *Deschampsia flexuosa* and stunted *Vaccinium myrtillus*. Other species present were *Anthoxanthum odoratum* (f.), *Agrostis tenuis* (o.f.), *Pteridium aquilinum* (o.), and the moss *Leucobryum glaucum* (f. to a.). *Lonicera* was frequent in the ground flora and was stunted in its growth, but occasionally occurred as a liane. This wood is of particular interest, as it is mentioned in a grant of land made by Prince Llewelyn to the monastery of Aberconway in the late twelfth century. The well-developed intact podsolic profiles in part of the wood suggest that it has escaped intense human interference.

The oak scrub of Bryn Mawr, about a quarter of a mile to the south of Coetmor wood, afforded an instance of the effect of parent material of the soil on its development and upon vegetation. The soils were of sedentary and colluvial origin from calcareous grits (Ordovician); the profiles examined were of a brown earth character, a rich brown colour throughout the profile being characteristic of them.

Quercus petraea dominated the wood with much *Corylus avellana* and a few scattered *Euonymus europaeus* bushes in the shrub layer. *Brachypodium sylvaticum* dominated the ground flora with *Mercurialis perennis* (o.-f.-l.f.), *Sanicula europaea* (o.), *Nepeta glechoma* (f.), *Viola riviniana* (f.), *V. hirta* (l.), *V. odorata* (l.); the latter two species were not in flower thus making it difficult to be certain of their identification. An outcrop of calcareous grits had *Helianthemum chamaecistus*, *Viola hirta* (?), *Trisetum flavescens*, *Pimpinella saxifraga*, and *Euonymus europaeus*.

Lunch was taken on the eminence of Bryn Mawr where a good view of the Conway Valley was obtained. Dr R. Elfyn Hughes pointed out the features of interest with regard to the human settlement of the valley.

In the afternoon Gorswen woods, near Roewen (about 4 miles south of Conway) were examined. Mixed Ordovician material (sedimentary, basic, and acidic volcanic rocks) in the form of drift, composed the parent materials of the soil, which showed no visible signs of podsolization, and it could be looked upon as a brown earth. The vegetation of the wood provided a contrast with those examined in the morning.

The hybrid *Quercus robur* × *petraea* was the most prominent tree, with *Q. robur* (o.-f.) and *Q. petraea* (o.), *Fraxinus excelsior* (o.-l.f.) and *Ulmus montana* (o.). Much *Corylus avellana* was present in the shrub layer, and the ground flora was distinctive in the abundance of *Mercurialis perennis* which formed the most prominent society. Locally, *Circaea lutetiana* was dominant. Other prominent species were *Sanicula europaea*, *Brachypodium sylvaticum*, *Geranium robertianum*, *Asperula odorata*, *Geum urbanum*, *Veronica montana* and *Stachys sylvatica*.

Soils of impeded drainage were prevalent, and these, as would be expected, were characterized by the presence of *Alnus rotundifolia*, and on the seasonally wet soils it was present with *Fraxinus excelsior*. Peaty soils were also present.

The derived vegetation, following felling of woodland of these wetter soils, was examined in marginal areas to the wood. *Molinia coerulea* communities were characteristic of them, in which the following species were prominent, *Carex panicea*, *C. flacca*, *C. fulva*, *C. echinata*, *C. lepidocarpa*, *C. pulicaris*, *Holcus mollis*, *Plantago lanceolata*, *Lotus major*, *Briza media*, *Eriophorum augustifolium*, *Juncus acutiflorus*, and *Sphagnum* species with *Aulocomnium palustre* and *Hypnum cuspidatum*.

It was pointed out that the pH of these wetter soils was not very low, ranging between pH 5 and 6. The possible native status of the mixed oak population was discussed by Dr R. Elfyn Hughes, who pointed out that this mixed character persisted on this type of soil up to the limits of woodland at about 1000 ft., where no evidence of planting is available.

After tea at Llanrwst, the party returned to Bangor via Bettws-y-Coed, Lake Ogwen, and Nant Ffrancon. At Ogwen a brief opportunity was taken to examine its littoral fauna and flora.

Two papers were read in the evening, the meeting being under the chairmanship of Prof. D. Thoday.

Prof. G. W. Robinson gave a short account of the soils of North Wales, illustrated by maps prepared by the Soil Survey. Typically the soils of the district are developed in drifts from acid igneous and hard Palaeozoic sedimentary rocks. They are generally deficient in lime and have a high organic matter status, which is mainly a consequence of the high rainfall and the prevailing grassland type of husbandry. One of the most important distinctions is between soils of free drainage and soils of impeded drainage. Although with freely drained soils the tendency is towards a podsolic type of profile, well-developed podsols are not common, partly on account of human interference and partly because of the comparative rareness of quartzose parent materials. Truncated profiles in which the surface soil is of B-horizon character are not uncommon in the foothills. The relative distribution of soils of free drainage and soils of impeded drainage is strongly influenced by surface relief.

Dr Charles E. Kellogg, Chief of the U.S. Soil Survey, was present and took part in the discussion.

Dr R. Elfyn Hughes gave an account of some of the soils of the woods examined during the day. Thus the first and second woods visited had distinctly acid soils, with marked base and phosphate deficiency, while the soils derived from the calcareous grits were not markedly acid nor base deficient, but were phosphate deficient. The soils of the mixed Ordovician glacial drifts (Gorswen woods) were moderately acid and base deficient, but had a markedly high phosphate status; these features persist in the zone of upland woodlands, where little evidence of podsolization is seen. The peat soils of the upland woodlands

are not distinctly acid—the pH's range between 5 and 6—and they are not markedly base deficient. They also have a good phosphate status. The ecological status of the woods in the north-west Conway Valley on the soils derived from mixed Ordovician glacial drift was discussed; the mixed oak population was considered to be a native character, while the ground flora showed intermediate features between that of *Quercetum petraeae* and *Q. roburis*, and the term *Q. intermedii* was tentatively suggested for them.

The status of the upland *Molinia* communities on peat of the upland woodland zone was also discussed, and transitional features between similar fen communities and those of bog were pointed out. The classification of British *Molinia* communities was briefly discussed.

The inter-relationships of plant communities, soil and microclimate were outlined for the zone of *Ulex gallii* acidic grasslands and heath in the Conway Valley. A specific range of plant communities occurs in relation to the genetic series of soils derived from the same parent material, and differs from other ranges of communities occurring in relation to different parent materials. The term 'Spectrum of Communities' was tentatively suggested to this specific range of plant communities, this 'spectrum' varying according to differences in parent materials of the soil, and microclimate. Specific instances were given to illustrate this.

In the short discussion that followed, Prof. Alun Roberts and A. C. S. Wright took part; the discussion was resumed by a small group on Sunday evening.

Saturday, 20 July

An excursion was planned to explore the woodlands of lower cwms of Snowdon, under the leadership of Mr N. Woodhead.

The thorough examination of the oak-ash woodlands of Nant Gwynant was prevented by a heavy deluge of rain, starting shortly after the party had left Hafod y Llan Farm (where the thanks of the Society were expressed to D. O. Williams, Esq.), but after a picnic-lunch, parties were able to examine the riverside meadows and upland moors. At Pen y Gwrhyd, the party examined the status of *Epilobium pedunculare*, now rapidly extending along ditches, walls and the closely cropped grassland.

The evening meeting, with Mr V. S. Summerhayes in the Chair, consisted of a symposium on the significance of historical studies in plant ecology, by Prof. R. Alun Roberts, Mr T. Jones Pierce, M.A. (Department of Welsh History, Aberystwyth) and Dr R. Elfyn Hughes. The following is a summary of the various contributions.

Prof. R. Alun Roberts: 'The study of semi-natural vegetation in certain areas of N. Wales with particular regard to historical factors is now being undertaken in the Department of Agricultural Botany at Bangor under the blessing of, and with the financial support of, the Agricultural Research Council. In prehistory the sequence of climate was all important. With the spread of human occupation pastoral and agricultural activities imposed a series of influences on vegetation that considerably modified the primary impress of climate.' The influence of the break up of the Tribal System under the Princes of Wales at the close of the medieval period and the consolidation of tenant holdings from then on to Tudor times are dealt with in Mr T. Jones Pierce's contribution to this symposium. The correlation of new human settlements in the fifteenth and sixteenth centuries and again in the eighteenth century with soil and geological factors in the Conway Valley and the effect of this on vegetation are dealt with by Dr R. Elfyn Hughes.

The peculiar economy of landholding under Welsh Tribal law in the Middle Ages with its marked transhumance from the lowlands to the uplands each season was demonstrated, and the early rise of tenant holdings by the middle of the sixteenth century shown. This consolidation did not occur in England until the days of enclosure in the eighteenth century. The peat enclosures in Wales in the eighteenth and nineteenth centuries were enclosures of wastes and rough hill and mountain grazings and not of arable.

As the volume of the trade in cattle to England from the fifteenth century onwards indicates, Wales was for centuries a cattle- and not a sheep-raising country. Evidence from estate records down the centuries, from inventories for probate purposes till the mid-nineteenth century and from enclosure awards, show that hill and mountain lands were stocked with cattle until the late eighteenth century, and that sheep farming only became prominent after large-scale enclosure from 1760 to 1830. The goat population exceeded that of sheep in certain fell areas till comparatively recent times. These areas can be correlated with the rocky nature of the terrain and the need for maintaining safe pasturage for

horned stock in rocky fell areas. The economy of hill farming after the repeal of the Corn Laws in the 1840's and the decline of flax, hemp, bere barley, and oats at high elevations and their effects on vegetation were examined together with the decline of hill farming from the depression of the 1870's. The effects of the withdrawal of cattle from the hills, and the decline of hay harvesting practice on upland *Molinia* swards, together with the effect of the decline in numbers of adult wether sheep in the present century on the hills and the ecological implications of the change in practices, are being recorded and examined.

Mr T. Jones Pierce gave an outline of the structure of the pastoral and agrarian organization of medieval Wales, stressing the intense morcellation that occurred of land holding, and the widely scattered holdings of individual tenant farmers.

The process of human settlement in relation to vegetation and soil types in the Conway Valley was described by Dr R. Elfyn Hughes. He dealt in particular with late medieval expansion, details of which have been worked out for the area from documentary evidence. Expansion of tribal holdings occurred at this period into areas of impeded drainage, thus suggesting that soils of free drainage were already fully occupied at an earlier period. It is, therefore, possible to suggest the likely date of origin of the majority of the subseral communities on soils of impeded drainage in the lowlands. Upland elder woodlands were penetrated into at a later period, i.e., the sixteenth century, clearing specifically being made for meadow-land, this being stimulated by the rise of the store cattle trade. The subseral *Molinia* communities which developed as a consequence of this are those which show transitional features between those of acid and fen peats; the presence of *Eriophorum latifolium*, *Briza media* and, locally, *Schoenus nigricans* stressing their nature. Hay cutting has continued since the clearing of the elder woodlands in the sixteenth century to within about 30 years ago. Thus, the precise time is known of the initiation of a subsere leading to the present-day community, under the deflecting influence of a specific form of human interference, i.e. hay cutting.

The intermediate nature of the *Molinia* communities is attributed to the prevalence in the district of basic intrusive and extrusive volcanic rocks.

The following took part in the discussion: V. S. Summerhayes, A. C. S. Wright, and F. Merton.

Sunday, 21 July

Following the Saturday evening account of the origin of the upland *Molinia* communities of the lateral valleys of the Conway, the party examined several widely scattered sites in the district itself to illustrate the facts brought forward. In the first instance, a *Molinia* meadow to the north of Pen y Gaer at an altitude of 900 ft. was studied. *Carex* species were very prominent, the chief being *C. panicea*, *C. lepido-carpa*, *C. fulva*, *C. pulicaris* and *C. dioica*. There was also much *Briza media*, and societies of *Eriophorum angustifolium*, *E. latifolium* and *Schoenus nigricans*. The legume *Lotus major* was also present.

The upland woodlands at altitudes of 800–1000 ft. on the banks of the River Dulyn were next examined, and here an opportunity was had of seeing the mixed oak population at high altitude. Scattered *Quercus robur*, *Q. petraea* and their hybrid being observed in *Molinia* grassland and also in birch woodland on drier soil near the farm of Rowlyn. The *Molinia* communities on peaty soils were essentially similar to the first site examined, those of the margin of the River Dulyn, known to have been elder wood in the sixteenth century, were marked by the prevalence of societies of *Eriophorum latifolium*, which was in full plume at the time. Societies of *E. angustifolium* were also present, but the two societies were distinct, little over-lapping of the two species occurring.

Monday, 22 July

Led by Profs. G. W. Robinson and R. Alun Roberts and Mr D. O. Hughes (Soil Survey of England and Wales), the party visited the Lleyn Peninsula of Carnarvonshire. The weather was initially showery, but later in the day cleared. The party, however, covered much ground, travelling over 100 miles during the day.

The first situation visited was an *Ulex gallii* wet heath to the west of Llanaelhaiarn. Gley podsols and peaty gleys were the prevailing soil types. Their parent material was glacial drift derived primarily from Ordovician sedimentary rocks. The vegetation type on the gley podsols was *Ulex gallii-Nardus stricta*

grassland with *Juncus effusus*, while on the peaty gleys some *Molinia coerulea* was present. The soils are recognized in the soil survey of Wales as a distinct series, designated the 'Ynys series'.

Soils derived from sandy glacial drift, an offshoot of the Irish sea drift mainly of Carboniferous origin, were next examined near Rhydyclafdy (Pwllheli). These soils are designated the 'Bodvel series' and they show a strong tendency to podsolization. A podsol conveniently exposed in a sand pit was demonstrated by Prof. Robinson and Mr D. O. Hughes. Sparse, heavily rabbit-grazed *Agrostis*-fescue grassland characterized the area, with bracken dominant over a considerable acreage. Instances of the wartime reclamation of this land were seen. Reseeding to grassland was done direct, reliance being placed upon *Dactylis glomerata*, which was found to be the most satisfactory species for this type of land; attempts at the establishment of *Medicago sativa* and *Lupinus* spp. were a failure.

Immediately marginal to the sandy area the semi-fen of Gors Geirch was visted and commented upon by Prof. Alun Roberts. Here distinct fen affinities were seen in the presence of *Cladium mariscus* and *Juncus subnodulosus* in the prevailing *Molinia* community. Other species of interest were *Carex lasiocarpa*, *Schoenus nigricans* and *Briza media*.

Near Aberdaron, the wet heath area of Rhoshirwaen (near the farm of Gorlan Hen) provided a contrast with sandy soils of Rhydyclafdy. The soil type here was known as the 'Dinas series'—these being rather heavy soils derived from the calcareous glacial Irish sea drift composed mainly of carboniferous material. In spite of the calcareous nature of the parent material of the soil, leaching due to high rainfall has occurred, and podsols and gley-podsols are prevalent. Mr D. O. Hughes exposed gley and gley podsolic profiles at the site visited. The vegetation type was a wet *Ulex gallii—Calluna vulgaris* heath, with much *Molinia coerulea*, *Carex panicea*, *C. flacca*, and *C. echinata*.

Tea was taken at Aberdaron, and following it the party visited the shore cliff exposures of the Irish sea drift. Its calcareous nature was stressed by the colonization of the exposed drift by *Anthyllis vulneraria* and *Brachypodium sylvaticum*.

On the return journey to Bangor, the dry heath slopes of Carnguwch, Llithfaen, were examined. Podsolic soils were prevalent with a vegetation of *Calluna vulgaris*, *Agrostis tenuis*, *Festuca ovina* and *F. rubra*, *Ulex gallii* and *Nardus stricta*. An extensive area of successful wartime reclamation from this type of land was also visited.

In the evening, at a meeting under the chairmanship of Prof. R. Alun Roberts, Mr N. Woodhead read a paper on the ecology of some common North Wales fresh-water algae, confining his remarks to the positions occupied by *Tabellaria ferestrata*, *T. flocculosa*, *Frustulia rhomboides*, and its variety, *saxonica*, *Synedra ulna* among the diatoms, *Cosmarium parvulum*, and *Netrium oblongum* variety *cylindricum* among the desmids. In North Wales these diatoms are as likely to attain maximum development in summer as in the colder months of the year, conversely the desmids are often freely active and abundant in midwinter, though they tend to show their distinctive maximum in September. He summarized the ecological and distributional data collected from a very wide range of habitats in Anglesey and Carnarvonshire during the last 15 years by Mr R. D. Tweed and himself. In the discussion that followed contributions were made by Prof. R. Alun Roberts (in the Chair), Prof. D. Thoday, Mr Summerhayes, and Dr Lund.

After the paper Mr Summerhayes expressed the thanks of the Society to Profs. Thoday and Alun-Roberts for the hospitality of their Departments, to Prof. Robinson for his help and guidance, especially on the Lleyn Peninsula excursion, to the staff of the various departments for helping to lead excursions and for the local knowledge which they made available to members and particularly to Dr R. E. Hughes without whose enthusiasm and organizing ability the meeting could not have taken place.

Those present left with very pleasant memories of an enjoyable four days, with a sincere appreciation of the valuable work which is being carried on at Bangor and elsewhere in the University of Wales, and certainly with an increased knowledge of Ecology in its many aspects.

LONDON MEETING

7 June 1947

By courtesy of Prof. Pearsall, F.R.S., a meeting of the Society was held on Saturday, 7 June 1947, in the Botanical Department, University College, London, at which Prof. Hugo Osvald of the Institute of Plant Husbandry of the University of Uppsala, Sweden, gave a paper on 'Toxic exudates from the roots of *Agropyron repens* (Couch-grass)'.*

Prof. Osvald, having been introduced by the President, opened his account by indicating the general direction of research upon weed problems in his Institute during the past 10 years. Weeds operate through competition upon crop plants and cause damage by effects upon the supply of water, mineral nutrients and light: they grow rapidly and stand drought well. It appears that some crops are weed-collecting and others not, and this apparently is associated with the way in which certain species can grow well together, whilst others are repellent to one another. In grass mixtures sown in Sweden in 1915–19 some grasses such as *Festuca rubra* and *F. duriscula* established almost pure and weed-free stands, and it seemed that the former in particular excluded the dandelion (*Taraxacum*): other grass mixtures gave very weedy crops. This was considered possibly due to the density and habit of the species concerned, but later *Arrhenatherum* on mineral soil was found to be remarkably weed-free, even in open stands. Both *Arrhenatherum* and *Dactylis* were thought to depress clover (*Trifolium*), even in moderately open crops.

In 1927 B. Hartwell described the result of work done at the experimental station, Rhode Island, on the residual effects of crop plants upon later crops, and ascribed the effects to alteration in the toxicity of aluminium ions in the soil. As early as 1832 de Candolle had put forward the theory that the grouping of plants in associations was due in part to toxic root exudates, but this was lost sight of in the enthusiasm with which Liebig's theory was taken up.

In recent times American workers took up work on soil toxins and toxic exudates: di-hydroxystearic acid was isolated from soil, and effects upon root systems similar to those now recognized as due to growth hormones were described. The recent demonstration and extraction of antibiotics from many categories of organism encouraged investigations of this kind.

In Uppsala, in the autumn of 1945, it was observed that in plots sown with winter rape, those which contained *Agropyron* showed little germination and poor development of rape, even though the couch was in very light density. In consequence of this observation an experiment was performed in which 'roots' of *Agropyron* were dried, ground, and extracted with water, this water being applied to germination tests of *Taraxacum* 'seeds'. Such extracts were found to have very strong toxic properties. Seeds of oats and of rape were also studied with extracts of *Agropyron* made with different solvents. Extraction was made at room temperature for a few hours and was followed by autoclave sterilization. Results were obtained of the kind given below:

Rape tested with water extract. 40 g. of powder extracted in 300 ml. water in cold for 2 hr. Concentrated to 100 ml., sterilized and applied to seeds treated to avoid moulds

	Water (%)	Extract (%)
Germination	88	8
Imbibed only	8	34
Healthy but ungerminated	0	29
Decayed	4	29

The effects produced on rape, oats, and peas by couch-grass extract were similar to those produced by hormones. In both instances there was first a stimulating effect and then a detrimental one, with injury appearing at a lower concentration in the roots than in the shoots. Very strong extracts led to a large

* An account of some of the results dealt with in Prof. Osvald's address will be found in 'Försök rörande Kampen mot Ogräset: 1935–46 (Weed control experiments)', *Växtodling (Plant Husbandry)*, 2. Uppsala, 1947, ed. H. Osvald. (With substantial English summaries.)

proportion of 'healthy ungerminated' seeds, and intermediate concentrations gave high proportions of decayed seeds. The extracts appear not to kill the seeds in the latter case, but to have made them susceptible to fungi, which seem themselves to be beneficially affected except at high concentrations. With increasing concentration of extract the effects are: diminished germination, abnormal shoots, decayed seeds, 'healthy but ungerminated' seeds, and the order of sensitiveness of the test plants is rape, oats, fungi.

From the improved extraction by aqueous ammonia it would seem that the toxic exudate is an acid; it is soluble in water and alcohol, little soluble in acetone, and almost insoluble in petrol ether. It will dialyse through certain membranes. It appears that in very low concentrations it may stimulate germination, and that seeds inhibited by the extract, after washing in water recover their power to germinate.

These results were held to justify the conclusion that the great competitive power of *Agropyron repens* is in part due to its root exudates, and it was proposed that the reason for resistance of some other species might well be due to the fact that they produce similar substances themselves.

Prof. Osvald concluded his account by remarking on the possible application of these results to various long-standing problems of horticulture, agriculture and ecology, especially mentioning the known inability of many species to compete with grasses, and the detrimental effects of grasses upon orchard trees.

This paper naturally provoked long and useful comment, a good deal of which turned upon the complex and conflicting nature of the grass-fruit tree relationship. In the discussion the following took part: Prof. A. R. Clapham, Prof. T. G. Tutin, Prof. W. H. Pearsall, Dr A. C. S. Wright, Dr E. W. Jones, Dr R. E. Hughes, Mr L. Layton, Mr W. C. Handley, Mr M. Chinner, Mr V. C. Tristram, Dr A. S. Watt, and Dr P. W. Richards.

In conclusion Prof. Pearsall expressed the thanks of the Society to Prof. Osvald for the substantial and striking nature of his address, and for the clarity of its exposition.

ANNUAL MEETING IN THE DEPARTMENTS OF BOTANY AND ZOOLOGY, BRISTOL UNIVERSITY

8–9 JANUARY 1948

Thursday, 8 January

The winter meeting of the Society opened on the afternoon of Thursday, 8 January. Members and guests assembled in the Department of Botany where an exhibition of ecological work had been arranged in two of the laboratories. The largest exhibit illustrated work on the hydrography and ecology of the Lough Ine Rapids, Co. Cork, the narrow and shallow channel connecting Lough Ine with Barloge Creek. A model of the Rapids on the scale of 0·5 cm. to 1 m. with a mechanism for raising and lowering the level of the water in Barloge Creek to correspond with the tidal changes, but timed so that 10 sec. represented 1 hr., demonstrated the complex situation very clearly; and various maps and charts illustrated further the hydrographical findings of the parties from Bristol University. The characteristic alga of the sublittoral fringe of the Rapids is *Himanthalia lorea* and diagrams showed the relation between the strength of current and the distribution of various animals on its buttons and straps. The small limpet *Patina pellucida* occurs more abundantly in moderate currents, but most of the other investigated animals prefer the more sheltered habitats near the ends of the Rapids. Other demonstrations showed analogous findings for the animals on various parts of the alga *Saccorhiza bulbosa* which occurs all over the floor of the Rapids except in the immediate vicinity of the actual sill (where it is replaced by *Laminaria digitata*), and which shows a striking variation in form with varying maximal strengths of current, the form of rapid currents having a long slender stipe with a much-divided narrow frond. The fauna of boulders was also demonstrated, some animals, such as *Sertularia operculata*, *Plumularia setacea* and *Corynactis viridis*, favouring strong currents; some, such as *Nassarius incrassatus* and *Bittium reticulatum*, being almost confined to quiet habitats; and

a few, including *Balanus balanus*, appearing indifferent to the variations in current. This most interesting and instructive demonstration also included specimens of some of the more striking constituents of the fauna, such as the Kerry Slug, known only from this part of the British Isles.

Botanical exhibits showed a transect of the dunes at Braunton Burrows, the line passing from the foreshore with *Salsola kali*, over a first dune ridge with *Ammophila*, *Carex arenaria* and *Ononis repens*, across a slack with tussocks of *Juncus acutus* and scattered *Scirpus holoschoenus* to a second dune ridge and then down to an eroded dune pasture with patches of *Pteridium*, a *Juncetum maritimi*, a *Salicetum repentis* and finally a *S. atrocinereae*. Chemical analyses showed a considerably higher calcium content in the first dune ridge and the slack than in the second dunes and the *Pteridietum*, but with no corresponding differences in pH. Dr Hope Simpson showed a series of photographs illustrating experiments initiated in 1939, when quadrats 2×2 m. were marked out on *Agrostis canina* turf on the clay-with-flints capping Butser Hill, Sussex, and were treated differently in respect of grazing, turf removal, and application of chalk. The marked preference of rabbits for chalked plots; the encouragement of *Agrostis tenuis*, *Digitalis* and *Ulex* and the elimination of *Galium saxatile* by chalking; and the very tardy recolonization of plots whose turf had been removed, were all made obvious. Finally, Dr Godwin demonstrated the results of investigations in the Somerset Levels where several Late Bronze Age trackways and curious small crannog-like wooden platforms have been shown to lie at the flooding horizon datable by pollen-analytical and archaeological evidence at *c.* 600 B.C. This and subsequent flooding horizons are characterized locally by the prevalence of remains of *Scheuchzeria palustris*, now no longer found in Britain except on Rannoch Moor.

Some 80 to 90 members and guests were present at a soirée held the same evening in the Department of Botany. After refreshments Dr Kitching showed a film illustrating both the work and relaxation of parties of students and members of staff of the Zoology Department, with collaborators from other departments and other Universities, during the excursions to Lough Ine. At the close of a most enjoyable evening the President, Dr A. S. Watt, expressed the thanks of the Society to Prof. M. Skene and Prof. J. E. Harris and the other members of staff of the two departments who had assisted in the preparations for entertaining the Society in so admirable a manner.

Friday, 9 January

At 10 a.m. on Friday, 9 January, the Annual General Meeting opened with the reading and signing of the minutes of last year's annual meeting, and with the reading of apologies for absence.

The report of the Hon. Secretaries upon the work of the Society in 1947 was read and accepted in the form already approved by the Council:

Report of the Hon. Secretaries for the year 1947

The Thirty-third Annual Meeting of the Society was held in the Department of Botany, University College, London, on Saturday, 11 January 1947. The business meeting at 11 a.m. was followed by Dr Watt's Presidential address on 'Pattern and Process in the Plant Community', and four other papers followed. About 100 members were present. A soirée and exhibition of ecological material had been displayed on the preceding Friday evening. The sincerest thanks of the Society are due to Prof. Pearsall for the extreme hospitality offered to the Society in the Department so long associated with us.

On 7 June Prof. Hugo Osvald of the Institute of Plant Husbandry in the University of Uppsala addressed a special meeting of the Society held in University College, London, upon 'Toxic exudates from the roots of *Agropyron repens* (Couch-grass)'. There was a large attendance, and the striking results reported excited much interest, so that a long and most profitable discussion followed.

After it had been found impossible to realize the Council's wish to hold a summer excursion in Scotland, the botanical and agricultural departments of University College, Bangor, very kindly undertook, at short notice, to be our hosts for the summer meeting. This was held between 18 and 22 July and, although attendance was small, those who came took part in a most gratifying series of conducted excursions in which Snowdon and the Lleyn Peninsula were visited, and the vegetation of the Conway Valley was thoroughly examined.

We are indeed grateful to Profs. Thoday, Alun-Roberts and Robinson for their kindness and especially to those who made the local arrangements, among whom we must specially mention Dr R. E. Hughes.

During the past year arrears of publication of the *Journal of Ecology* have to some extent been overtaken. Parts 1 and 2 of volume 34 appeared respectively in February and August, and the editor, acting on instruction from the Council, prepared volume 35 (that belonging properly to the year 1947), as a single issue containing two parts. This is now on the point of publication. Volume 34 contained 252 pages with eleven original articles, together with obituary and other notices, reviews, and three parts of the Biological Flora. Volume 35 contains 308 pages with twelve original articles, and also reviews, notices, and four parts of the Biological Flora.

The first number of volume 16 of the *Journal of Animal Ecology* appeared in May, containing 114 pages, with eight original articles, reviews, and the usual notices of publications on Animal Ecology. The publication of the second number has been delayed by publishing difficulties, but it is expected early this year, and will contain about 125 pages with seven original articles, one review and notices.

Since the last Annual Meeting the membership of the Society has risen from 502 to 550 members. Eleven members have resigned or died, and 58 new members have been elected. Of the present membership 287 members take the *Journal of Ecology* alone, 168 the *Journal of Animal Ecology* alone, 92 members receive both *Journals*, and 3 neither.

Publication of the Biological Flora continues satisfactorily in the hands of the editors appointed by the Council, namely Prof. A. R. Clapham, Dr P. W. Richards and the Editor of the *Journal of Ecology*. In the forthcoming issue of the *Journal of Ecology* there are accounts of the genus *Melandrium*, of *M. album*, *M. dioicum*, *Suaeda maritima* and *S. fruticosa*.

<div align="right">

H. GODWIN ⎱ *Hon. Secretaries*
L. A. HARVEY ⎰

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The Hon. Treasurers gave a provisional report of the financial position of the Society, pointing out the difficulties of making any definite statement but drawing attention to an improvement in income from increases in membership and collected subscriptions and from the sale of back numbers of the *Journals*. They estimated that, despite the still increasing costs of publishing the two *Journals*, there would be a surplus of about £160 on the year's working, but they warned the Society against complacency over the financial situation. The *Journal of Ecology* was a year in arrears of publication, volume 35, properly due in 1947, being expected to appear, as one double part, early in the current year, 1948. Publication of parts of a second volume (36) and the reprinting of certain back numbers in the same year would absorb a good deal of the Society's fluid funds. Still increasing costs of publication might be met in part by increased membership and sales, but since the Council did not propose to reduce the size of the *Journals*, but rather to restore them to their pre-war size, it was likely that the subscriptions to members must be raised. The necessary increase could not be assessed until there was some stabilization of costs, and no steps would be taken at present.

Prof. W. H. Pearsall proposed that the Society should express its thanks to the Hon. Treasurers for their devoted work under exceptionally difficult conditions, and this was seconded and carried unanimously. Dr H. Godwin proposed and it was agreed that Messrs Wm. Norman and Sons be reappointed the Society's auditors; and on the proposal of Mr V. S. Summerhayes, it was agreed that the annual grant of £10 to the Freshwater Biological Association should be renewed in 1948. Mr H. Cary Gilson expressed on behalf of the Freshwater Biological Association his appreciation of this grant.

Prof. W. H. Pearsall expressed his pleasure that the Society's obligation to its members would be discharged less tardily than during recent years by the imminent publication of a double number (vol. 35) of the *Journal of Ecology* for 1947. This volume would almost exhaust material in hand, and, drawing attention to the fact that the *Journal* had been largely supported of late by overseas contributors, he appealed to British members to submit papers for publication in the *Journal*.

Mr C. Elton stated that the greater volume of wartime research in animal ecology had enabled the *Journal of Animal Ecology* to be less dependent on overseas contributors than was the *Journal of Ecology*, but he asked for more papers on invertebrates and especially on insects, and more on fresh-water and marine ecology so that it might be possible to maintain a just balance between the various branches of the subject.

Prof. A. R. Clapham, dealing with the Biological Flora, stated that the publication of three accounts in volume 34 brought the total number of published accounts to twenty-two. Four more were in print and would appear soon in volume 35, others were in manuscript and in the editors' hands, and some two hundred were in preparation. He appealed for a more rapid preparation of shorter accounts so that a greater number could appear in each future volume.

The meeting then proceeded to the election of Officers as follows:

President: C. ELTON.
Vice-Presidents: G. C. VARLEY, V. S. SUMMERHAYES.
Hon. Secretaries: A. R. CLAPHAM, L. A. HARVEY.
Hon. Treasurers: V. S. SUMMERHAYES, A. S. WATT.
Hon. Editors: H. GODWIN, C. ELTON.
Ordinary Council Members: W. H. PEARSALL, O. W. RICHARDS, E. ASHBY.

Dr A. S. Watt expressed from the Chair the Society's great debt of gratitude for the services of the retiring Hon. Secretary, Dr H. Godwin, and the retiring Hon. Editor of the *Journal of Ecology*, Prof. W. H. Pearsall, and the Society acknowledged his statement with acclamation.

At about 11 a.m. the new President, Mr C. Elton, took the Chair, and Mr R. Bassindale opened the series of papers on 'Investigations of the Lough Ine Rapids: a study of the distribution of marine organisms in relation to the water-current' with an account of the 'Hydrography' of the Rapids. Lough Ine, 1 km. long by 0·6 km. wide, and up to 52 m. deep, with very little fresh water draining into it, was connected with the open sea of Barloge Creek by the narrow channel of the Rapids, only 20–30 m. wide and 1–2 m. deep. The first task of the visiting parties had been to sound and contour the Rapids, which were found to be shallower at a sill near the centre. The smallness of the connecting channel had curious effects on the tidal régime in the Lough, causing a smaller tidal range there, a period of outflow twice as long as that of inflow, and a level of low-water springs higher than that of low-water neaps. Current speeds were measured by means of floating bottles and the Watt's meter, and it had been possible to draw diagrams showing the current speed in the Rapids at any level and at any time. Maximal current speeds were always on the downstream side of the sill, and reached 6 knots on outflow. There was a greater flow through the Rapids than in the Tees in winter. Data were checked by calculations from the tidal swing in the Lough, and the agreement was excellent. All the main features were reproduced in the model which had been exhibited the previous evening.

Mr F. J. Ebling followed with an account of '*Saccorhiza* and its fauna'. *Saccorhiza* was the dominant alga all over the floor of the Rapids but was replaced by *Laminaria digitata* in the neighbourhood of the sill, where maximal current velocities reached 2·6 m./sec. in the 'canopy' formed by algae. Biometric studies of *Saccorhiza* showed increasing overall length, stipe length and basal angle of frond with increasing weight of the individual up to a point, but the pitch of the curves varied with current, lengths being greatest and basal angle smallest, for similar weights, in the fastest currents. Of the four sedentary Polyzoa on *Saccorhiza* which were studied, *Membranipora membranacea*, *Hippothoa hyalina*, and *Tubulipora porosa* showed maximal numbers in regions of moderate current, while young Anomiids were almost restricted to quiet regions: some found shelter on the frills of the alga even in the sill region. Of motile forms the Gastropods *Gibbula cineraria* and *Bittium reticulatum* were only in quiet water, the amphipod *Jassa falcata* was chiefly in the sill region, while the limpet *Patina pellucida* preferred moderate currents.

Dr Purchon, of Cardiff, concluded the series with a brief analysis of the factors which might account for the observed distributions. He supposed that current velocity was the only important variable factor, and suggested that strong currents might operate mechanically by making it impossible for larvae to settle or metamorphose and for adults to maintain their position, or by impairing the food-collecting mechanisms; that variations in the volume of water passing might affect the total numbers of larvae or of food-plankton reaching a given point; and that there might be indirect biological influences through the presence of suitable substrata or food-bases, or through variations in the numbers of predators and of competitors for food or space. Some of these factors had been explored experimentally and other experiments were in course of preparation. In a lively discussion Mr G. M. Spooner, Mr L. A. Harvey, Mr R. W.

Butcher, Dr G. C. Varley, Mr C. Elton, Dr H. Godwin, Mr H. Cary Gibson, Dr J. F. Hope-Simpson and Dr D. H. Valentine took part.

The afternoon session opened with Mr A. D. Bradshaw giving an account of 'Ecological observations on the two British hawthorns', made by himself and Mr R. L. Cuany. A 'leaf indentation index', the ratio of the total length of indentations to the sum of the length and breadth of the leaf, was found to be closely correlated with other differential characters, and was used in analysing mixed populations of hawthorns. Belt transects from open hawthorn scrub into the interior of closed woods on base-rich clays in the Weald and in Cambridgeshire gave very consistently a high indentation index (corresponding with more or less pure *monogyna* populations) outside, an intermediate value on the wood-margin and low values (corresponding more nearly with pure *oxyacanthoides*) in the wood interior. In more open woods, such as Buff Wood in Cambridgeshire, the index in the interior was more variable and less low on the average. The forms with high index were shown to be the earliest colonizers of gaps, and were found to survive but not to flower in shade. In some shaded localities the forms with high index were tree-like in habit while those with low index were shrub-like. It was concluded that *Crataegus monogyna* is the form adapted to open communities and *C. oxyacanthoides* that of closed woods. Human exploitation has favoured *monogyna* at the expense of *oxyacanthoides*, which is now rarely found in pure populations; and has encouraged hybridization with production of the fertile intermediates which occur so commonly in many areas. Mr Cuany, Profs. G. E. Blackman, W. H. Pearsall and A. R. Clapham, Mr C. Elton, Mr H. G. Baker, Dr E. F. Warburg, Mr V. S. Summerhayes, Dr A. S. Watt, Mr A. J. Wilmott and Dr H. Godwin took part in an active discussion. Dr R. L. Crocker followed with a paper on the 'Relationship of soil, vegetation and climate in S. Australia', in which he pointed out the comparatively slight interference suffered by the vegetation of S. Australia before the advent of white men. The present distribution of vegetation was determined partly by climate but partly also by soil type, areas of common soil type extending along climatic gradients and of differing soil types in the same climatic region permitting the separation of the effects of the two major factors. Along a climatic gradient the relevant climatic factors exerted a gradual sifting effect, various ecologically important species entering and dropping out according to their various ranges of tolerance; but juxtaposed soil types brought about abrupt changes in vegetation. It was important not to stress unduly the concept of the climatic climax and of the post- and pre-climax in interpreting the vegetation of areas where edaphic control was so significant. An interesting discussion followed, with Profs. T. G. B. Osborn and W. H. Pearsall, Mr C. Elton, Dr D. H. Valentine, Dr R. E. Hughes and Dr H. Godwin as contributors.

The last paper was by Mr H. G. Baker on 'Historical-geographical relationships of *Armeria* and related genera'. The two British species of *Armeria* were dimorphic in the sense that both consisted of two kinds of plants, differing in the ornamentation and usually also in the size of their pollen-grains, and in the prominence of their stigmatic papillae. Type A plants had coarsely reticulate pollen and obscurely papillate ('cob') stigmas, while in the Type B plants the pollen-grains were finely reticulate and usually smaller, and the stigmas had strongly projecting papillae ('papillate'). The plants were self-incompatible. Late glacial finds of *Armeria* from Ireland and from Nazeing in the Lea Valley have been reported by Prof. K. Jessen and Dr H. Godwin respectively to show dimorphism, so that the widespread late glacial *Armeria* resembled *A. maritima* rather than the monomorphic Arctic species. Of the British species of *Limonium*, *L. vulgare* ($2n = 32$), *L. lychnidifolium* ($2n = 16$), and *L. bellidifolium* ($2n = 18$) were dimorphic, while *L. binervosum* ($2n = 32$) and *L. humile* ($2m = 36$) were monomorphic and self-compatible forms, the former A-cob, the latter A-papillate and agreeing with N-E. American, not with European, species. It was of interest that only self-compatible (or ?apomictic) species occurred on both sides of the Irish Sea, and that the highly variable and taxonomically troublesome *binervosum* complex should be monomorphic and probably apomictic in the British Isles, though not throughout its range. Mr Baker suggested that the crossing of a sea-barrier like the Irish Sea presented great difficulties to a dimorphic self-incompatible species. Dr D. H. Valentine and Mr A. J. Wilmott took part in a lively discussion, particularly about the taxonomic status of the anomalous *L. paradoxum*.

The President closed by thanking Profs. M. Skene and J. E. Harris and their staffs for a most enjoyable meeting, the members of the Society signifying their hearty agreement.

BIOLOGICAL FLORA OF THE BRITISH ISLES

ACCOUNTS PUBLISHED OR IN PREPARATION

The parts already published are:

Juncus L., by P. W. Richards and A. R. Clapham. *J. Ecol.* **29**, no. 2.

J. inflexus L., by P. W. Richards and A. R. Clapham. *J. Ecol.* **29**, no. 2.

J. effusus L., by P. W. Richards and A. R. Clapham. *J. Ecol.* **29**, no. 2.

J. conglomeratus L., by P. W. Richards and A. R. Clapham. *J. Ecol.* **29**, no. 2.

J. subnodulosus Schrank, by P. W. Richards and A. R. Clapham. *J. Ecol.* **29**, no. 2.

*Zostera L., *Z. marina* L. and *Z. hornemanniana* Tutin, by T. G. Tutin. *J. Ecol.* **30**, no. 1.

Cladium mariscus R.Br., by V. M. Conway. *J. Ecol.* **30**, no. 1.

Aster tripolium L., by A. R. Clapham, W. H. Pearsall and P. W. Richards. *J. Ecol.* **30**, no. 2.

Juncus filiformis L., by P. W. Richards. *J. Ecol.* **31**, no. 1.

J. macer Gray, by P. W. Richards. *J. Ecol.* **31**, no. 1.

*Rhamnus cathartica L. and *Frangula alnus* Mill., by H. Godwin. *J. Ecol.* **31**, no. 1.

Tamus communis L., by I. H. Burkill. *J. Ecol.* **32**, no. 1.

Acer campestre L. and *A. pseudo-platanus* L., with a note on *A. platanoides* L., by E. W. Jones. *J. Ecol.* **32**, no. 2.

*Polygonum L. em. Gaertn., *P. persicaria* L., *P. lapathifolium* L. and *P. petecticale* (Stokes) Druce, by N. W. Simmonds. *J. Ecol.* **33**, no. 1.

Gentiana pneumonanthe L., by N. W. Simmonds. *J. Ecol.* **33**, no. 2.

Allium vineale L., by Mrs Ruth H. Richens. *J. Ecol.* **34**, no. 1.

Atropa belladonna L., by R. W. Butcher. *J. Ecol.* **34**, no. 2.

Glyceria maxima (Hartm.) Holmb., by J. M. Lambert. *J. Ecol.* **34**, no. 2.

*Melandrium (Roehling em.) Fries, *M. album* (Mill.) Garke, and *M. dioicum* (L. emend.) Coss. and Germ., by H. G. Baker. *J. Ecol.* **35**, nos. 1 and 2.

Suaeda maritima (L.) Dum., by V. J. Chapman. *J. Ecol.* **35**, nos. 1 and 2.

Suaeda fruticosa Forsk., by V. J. Chapman. *J. Ecol.* **35**, nos. 1 and 2.

*Sonchus L., *S. oleraceus* L. emend. Gouan, and *S. asper* (L.) Hill by R. A. Lewin. *J. Ecol.* **36**, no. 1.

These may be obtained from the Cambridge University Press, 200 Euston Road, N.W. 1, at 1*s.* each; those marked with an asterisk are sold as double parts, 2*s.* Standing orders for all parts issued may be placed at the reduced price of 9*d.* each, double parts 1*s.* 6*d.*

The following are being prepared:

Aconitum anglicum Stapf, H. A. Hyde, National Museum of Wales, Cardiff.

Adoxa moschatellina L., Prof. M. Skene, The University, Bristol.

Alchemilla vulgaris agg., *A. alpina* L., and *A. conjuncta* Bab., S. M. H. Walters, The Botany School, Cambridge.

Allium paradoxum G. Don, R. S. C. Aytoun, 81 Dalkeith Road, Edinburgh 9.

A. ursinum L., T. G. Tutin, University College, Leicester.

Anagallis arvensis L. and *A. foemina* Mill., J. L. Crosby, Department of Botany, The University, Durham.

Andromeda polifolia L., Prof. W. H. Pearsall, F.R.S., Department of Botany, University College, Gower Street, W.C. 1.

Anemone nemorosa L., A. C. Crundwell, Loadhams, Farnham, Surrey.

Arbutus unedo L., Dr D. A. Webb, Trinity College, Dublin, and J. R. Sealy.

Arenaria verna L., Dr K. Blackburn, King's College, Newcastle-on-Tyne.

A. norvegica Gunn., Dr W. A. Clark, King's College, Newcastle-on-Tyne.

Arum maculatum L., F. A. Sowter, 9 North Avenue, Leicester.

Asperula odorata L., Prof. A. R. Clapham, Department of Botany, The University, Sheffield.

Astragalus alpinus L., Miss E. J. Drew, Balavoulin, Pitlochry, Perthshire.

Blackstonia perfoliata (L.) Huds., Dr B. Colson, University Department of Botany, Reading.

Carex acutiformis Ehrh., *C. bigelowii* Torr., *C. curta* Good., *C. disticha* Huds., *C. riparia* Curt., and *C. saxatilis* L., E. Vernon Watson, University Department of Botany, Reading.

Carex flacca Schreb., F. J. Taylor, University College, Leicester.

Carlina vulgaris L., *Cirsium palustre* (L.) Scop. and *C. vulgare* (Savi) Airy-Shaw (*C. lanceolatum* (L.) Scop.), Dr W. A. Sledge, University Department of Botany, Leeds, 2.

Clematis vitalba L., O. Polunin, Charterhouse, Godalming.

Colchicum autumnale L., Dr R. W. Butcher, Culford House, Ewe Lamb Lane, Bramcote, Notts.

Corallorrhiza trifida Châtel., Prof. J. R. Matthews and Dr Downie, University Department of Botany, Old Aberdeen.

Cornus sanguinea L., J. W. Wilson, Department of Botany, Oxford.

Cuscuta europaea L., Bernard Verdcourt, 86 Claremont Road, Luton, Beds.

Danaa cornubiensis (L.) Burnat, Dr G. Pethybridge, Penlee, Harleigh Road, Bodmin.

Daphne laureola L., Dr P. W. Richards, The Botany School, Cambridge.

Drosera rotundifolia L., *D. anglica* Huds. and *D. longifolia* L., Miss A. A. Jeffares, Trinity College, Dublin.

Elymus arenarius L., T. E. T. Bond, Tea Research Institute, Ceylon.

Epilobium pedunculare A. Cunn., Miss A. J. Davey, Department of Botany, Memorial Buildings, Bangor.

Eriocaulon septangulare With., Dr Leighton Hare, Jodrell Laboratory, Royal Botanic Gardens, Kew.

Galium debile Desv., *G. palustre* L. and *G. uliginosum* L., A. C. Crundwell, University Department of Botany, Oxford.

G. erectum Huds. and *G. mollugo* L., Miss M. Priestley, c/o The Botany School, Cambridge.

Glaux maritima L., Miss C. M. Gibson, Municipal College, Portsmouth.

Glyceria declinata Bréb., *G. plicata* Fr. and *G. fluitans* (L.) R.Br., Miss J. M. Lambert, Westfield College, Hampstead, N.W. 3.

G. maxima (Hartm.) Holmb., Miss J. M. Lambert, Westfield College, Hampstead, N.W. 3.

Goodyera repens R.Br., Prof. J. R. Matthews and Dr Downie, University Department of Botany, Old Aberdeen.

Helictotrichon (Avena) pratense (L.) Pilger and *H. pubescens* (Huds.) Pilger, Dr G. Carson, School of Agriculture, Cambridge.

Juncus articulatus L., em. Wahlenb. and *J. acutiflorus* Ehrh. ex Hoffm., Prof. A. R. Clapham, Department of Botany, The University, Sheffield.

J. squarrosus L., Prof. W. H. Pearsall, F.R.S., University College, Gower Street, London, W.C. 1.

J. triglumis L., Dr W. A. Clark, King's College, Newcastle-on-Tyne.

Juniperus communis L., T. G. Tutin, University College, Leicester.

Leontodon leysseri (Wallr.) Beck. (*Thrincia hirta* Roth.) and *L. hispidus* L., Dr K. Blackburn, King's College, Newcastle-on-Tyne.

Leucojum aestivum L., Dr F. B. Hora, University Department of Botany, Reading.

Limosella aquatica L., Dr F. W. Jane and Miss R. Dowling, Department of Botany, University College, Gower Street, London, W.C. 1.

·*L. subulata* Ives, Dr K. Blackburn, King's College, Newcastle-on-Tyne.

Listera cordata (L.) R.Br., Prof. J. R. Matthews, University Department of Botany, Old Aberdeen.

Lloydia serotina (L.) Reichb. and *Lobelia dortmanna* L., Dr N. Woodhead, University Department of Botany, Bangor, North Wales.

Luzula forsteri (Sm.) DC. and *L. pilosa* (L.) Willd., Prof. T. Harris, University Department of Botany, Reading.

L. sylvatica (Huds) Gaud., Miss E. M. Leyland, 25 Devon Street, Barrow-in-Furness, Lancs.

Myosotis arvensis (L.) Hill, *M. collina* Hoffm. and *M. versicolor* Sm., A. E. Wade, National Museum of Wales, Cardiff.

M. alpestris Schmidt, M. E. D. Poore, Clare College, Cambridge.

Myrica gale L., Miss A. J. Davey, Department of Botany, Memorial Buildings, Bangor.

Naias flexilis Rostkov, Prof. J. W. Heslop Harrison, F.R.S., King's College, Newcastle-on-Tyne.

Narcissus pseudo-narcissus L., Dr J. Caldwell, University College, Exeter.

Nardus stricta L., Dr R. Elfyn Hughes, Department of Agricultural Botany, Bangor.

Narthecium ossifragum (L.) Huds., Dr Mollison, University Department of Botany, Old Aberdeen.

Nasturtium officinale R.Br., H. W. Howard, School of Agriculture, Cambridge.

Obione portulacoides (L.) Moq., and *O. pedunculata* (L.) Moq., Prof. V. J. Chapman, c/o The Botany School, Cambridge.

Ophrys arachnites Hoffn., Francis Rose, The Forge House, East Malling, Kent.

Orchis fuchsii Druce, *O. elodes* Gris., *O. latifolia* L. sec. Pugsl. (*O. incarnata* auct. angl.) and *O. purpurella* Stephenson, Prof. J. W. Heslop Harrison, F.R.S., King's College, Newcastle-on-Tyne.

O. purpurea Huds., Francis Rose, The Forge House, East Malling, Kent.

Oxalis acetosella L., Miss Ethel Bolton, King's College, Newcastle-on-Tyne.

Potamogeton coloratus Hornem., *P. filiformis* Pers. and *P. pectinatus* L., Prof. J. W. Heslop Harrison, F.R.S., King's College, Newcastle-on-Tyne.

P. gramineus L. and *P. rutilus* Wolfg., Dr W. A. Clark, King's College, Newcastle-on-Tyne.

Quercus robur L. and *Q. petraea* (Mattuschka) Liebl., Dr E. W. Jones, Imperial Institute of Forestry, Oxford.

Ranunculus acris L., Miss M. S. Campbell, 5 Addison Crescent, London, W. 14.

R. ficaria L., B. S. Young, 29 Montana Road, Tooting Bec, London, S.W. 17.

R. lingua L., W. B. Hornby, Park Lawn, The Park, Cheltenham.

R. aquatilis agg., Dr R. W. Butcher, Culford House, Ewe Lamb Lane, Bramcote, Notts.

Rhynchospora laba (L.) Vahl and *R. fusca* (L.) Ait. f., Miss E. Canton, Department of Biology, Technical College, Sunderland.

Rosa spp. (excl. *R. arvensis, micrantha* and *tomentosa*), Prof. J. W. Heslop Harrison, F.R.S., King's College, Newcastle-on-Tyne.

Rumex spp., J. E. Lousley, 7 Penistone Road, Streatham Common, S.W. 16.

Saxifraga spp. (mossy), Dr D. A. Webb, Trinity College, Dublin.

Saxifraga spp. (Robertsonian), Dr D. A. Webb, Trinity College, Dublin, and B. L. Burtt, The Herbarium, Royal Botanic Gardens, Kew, Surrey.

Scilla non-scripta (L.) Hoff. & Link, Prof. G. E. Blackman, Department of Rural Economy, Oxford.

Sedum acre L., Dr B. Barnes, Department of Biology, Chelsea Polytechnic, London, S.W. 3.

Sinapis arvensis L., G. E. Fogg, Department of Botany, University College, Gower Street, W.C. 1.

S. palustris L., Francis Rose, The Forge House, East Malling, Kent.

Sorbus spp., Dr E. F. Warburg, Bedford College, Regent's Park, N.W. 1.

Spiranthes stricta Nels., Prof. J. W. Heslop Harrison, F.R.S., King's College, Newcastle-on-Tyne.

Stellaria nemorum L., Dr K. Blackburn, King's College, Newcastle-on-Tyne.

Subularia aquatica L., Dr N. Woodhead, Department of Botany, Bangor.

Thlaspi alpestre L., Dr K. Blackburn, King's College, Newcastle-on-Tyne.

Tilia cordata Mill. and *T. platyphyllos* Scop., H. A. Hyde, National Museum of Wales, Cardiff.

Trientalis europaeus L., Prof. J. R. Matthews, University Department of Botany, Old Aberdeen.

Ulmus spp., Dr R. Melville, The Herbarium, Royal Botanic Gardens, Kew.

Urtica spp., P. Greig-Smith, Department of Botany, The University, Manchester.

Vaccinium vitis-idaea L., P. A. Tallentire, 14 Hulme Hall Avenue, Cheadle Hulme, Cheshire.

Valeriana officinalis L. and *V. sambucifolia* Mikan, J. Carpenter, Department of Botany, King's College, Strand, W.C. 2.

Veronica anagallis-aquatica L., *V. aquatica* Bernh., and *V. beccabunga* L., J. H. Burnett, Department of Botany, Oxford.

Viburnum lantana L. and *V. opulus* L., Dr H. Godwin, The Botany School, Cambridge.

Viola lutea Huds. and *V. tricolor* L., Dr P. E. Fothergill, King's College, Newcastle-on-Tyne.

Wahlenbergia hederacea Reichb., Francis Rose, The Forge House, East Malling, Kent.

The assistance of members of the Society will be greatly welcomed by the authors who are preparing these accounts. Information should be sent direct to the addresses given above. Anyone wishing to write an account singly or in collaboration should communicate with one of the members of the Committee or with the Hon. Secretary of the Society.

Accounts ready for publication should be sent to Dr P. W. Richards, The Botany School, Cambridge.

BIOLOGICAL FLORA OF THE BRITISH ISLES

Sonchus L.
(S. oleraceus L. and S. asper (L.) Hill)

RALPH A. LEWIN

The genus *Sonchus* L. (excl. *Mulgedium* Less.) includes four British species, two perennial, with large flower-heads (*Sonchus arvensis* L. and *S. palustris* L.) and two annual, with flower-heads about 2 cm. in diameter. These last were grouped together (as '*S. oleraceus*') by Linnaeus, but there appears no doubt that *S. oleraceus* L. em. Gouan and *S. asper* Hill are quite distinct species. The character of the achenes provides the clearest criterion for their differentiation, but a number of other characters serve readily to distinguish the species when ripe fruits are not present. (These features will be described below under *S. asper*.) Nevertheless, the close relationship of the two species is shown not only by their general similarity in morphology and ecology, but also by the homologous variations which they exhibit (cf. Vavilov, 1922). It may be postulated that *S. oleraceus* ($2n = 32$) is a tetraploid* and *S. asper* ($2n = 18$) a tetrasomic diploid: guard cell and pollen grain volumes of the two species are in the approximate ratio of 2 : 1.

Both species are weeds—'anthropophytes'—*par excellence*, which have followed the spread of civilization to the temperate and sub-tropical zones of both hemispheres and to high altitudes in the tropics, until their present distribution is world-wide, extending between the Arctic and Antarctic circles.

Note on the colour of the achenes

In both species, as in *S. arvensis*, the ovaries typically develop a yellow coloration within 3 or 4 days of pollination, and a day or so prior to the dispersal of the ripe achenes the pericarp darkens to brown. As a rule, the achenes in *S. asper* are of a less deep colour than are those of *S. oleraceus*: in the latter species the marginal achenes of the receptacle are of a greenish grey shade, considerably paler than those of the rest of the disk.

A variety of *S. asper*, not uncommon throughout Great Britain, lacks the yellow colour in the unripe achenes, and on dispersal these are of a pale fawn colour. Ellis (1944) has recorded this variety growing in wet places in Norfolk: he also states that fruits of *S. palustris* likewise do not pass through a yellow stage on ripening. A corresponding variety of *S. oleraceus* was found in Guernsey, Channel Isles, in 1946, but is evidently very rare. Plants of *S. asper* with white achenes are common in the Orkney Isles and in the north and west of Scotland. A rare variety of this species, found at Ballachulish, Argyll in 1942 and 1943, and on the islands of Benbecula (1945) and Guernsey (1946), has olivaceous achenes, the yellow colour of the developing ovaries soon becoming suffused with green, which darkens when the fruit becomes ripe. A variety of *S. asper*, with very dark brown achenes, is probably widespread. Corresponding colour varieties, other than the fawn variety mentioned above, have not been found in *S. oleraceus*. Variation is also shown in the width of the achene 'wing'—vide illustrations in Korsmo (1935) and Pammel (1913).

Since these characters are constant in cultivation, there seems little reason to doubt that they are controlled by genes similar to those responsible for the different achene colours in *Lactuca sativa* (Thompson, 1943).

* There is some evidence of secondary association of bivalents on the metaphase plate in the first division of the pollen mother cells—cf. Cooper & Mahoney (1935).

Sonchus oleraceus L. emend. Gouan

Sonchus oleraceus may be classed as a summer or a winter annual according to the time of germination of the achenes. The stem is commonly 20–150 cm. in height, hollow, septate at the nodes, and more or less pentagonal in section by reason of the decurrent midribs of the leaves. The latter are never spinous or glossy (as in *S. asper*), and, even

Fig. 1. *Sonchus oleraceus* L. Vice-comital distribution in the British Isles and (inset) distribution in Europe.

KEY. Broken line: limit of isolated records. Continuous line: limit, south of which plant is relatively common.

on the same plant, are very variable in form. In the leaves at the base of the stem, the lamina is ovate and petiolate: in passing up the stem the petiole becomes winged, with enlarged, acute, spreading auricles, while the lamina is runcinate-pinnatifid: and below the inflorescence the 'lamina' region is reduced as the petiolar wings widen. Finally,

the leaves become small and bractlike where they subtend the upper flowering branches, the form of these upper bracts being even more variable than that of the stem leaves. The plant is glabrous except for a caducous tomentum around the young leaf- and flower-buds, and glandular hairs which may be present on the branches and involucres of the inflorescence.

The inflorescence is irregularly cymose-umbellate. The involucres are about 1·5 cm. long, and the span of the capitulum when open is about 2–2·5 cm. The outer involucral bracts are shorter and more acute than the inner. The florets are all ligulate, with 4–5 terminal teeth: they are yellow, the outer florets in addition being tinged with purple on the dorsal side. The anthers are tipped with grey: the stigmata are likewise grey. The pappus is white and silky, consisting of two zones of differentiated hairs.

S. oleraceus subsp. *angustissimus* (Lindberg, 1932) is described from the Atlas Mountains, N. Africa. The plant illustrated shows some resemblance to the Mediterranean species *S. tenerrimus*: its status within the species considered here is doubtful.

Preliminary culture experiments have indicated that ecotypes occur, but no clearly defined varieties have been recognized.

S. oleraceus var. *gracilis* Schwartz A. is an obvious shade form: and no doubt much of the variation in leaf shape is environmentally, as well as genetically, controlled (cf. Villars, 1789). The winter rosette form is probably induced by short-day illumination in autumn (vide II (a)).

A large number of varieties has been described, but without a genetical analysis of the factors involved, the names which have been given are of small value. Ostenfeld (1917) describes constant heritable variation in four features—leaf shape, flower colour, the presence of glandular hairs on the stem (subvar. *glandulosus* Cosson & Germain (1845) *et al.*), and of similar processes on the involucral bracts. Zenari (1921, 1924), after several years of cultivation experiments, found no constancy in the occurrence of glandular hairs* but likewise describes varieties of leaf form and flower colour. Druce (1926) makes some preliminary observations on the constancy in culture of leaf-form varieties: the present author has also observed a series of heritable characters in achene colour, and variations (purple and yellow) in the colour of the glandular hairs.

These features vary to a large extent independently, and may closely parallel variations in *S. asper*, and in *Lactuca* spp.: in the latter species, leaf form, colour of leaves and achenes, etc. have been investigated genetically (Thompson, 1943).

Ostenfeld, while recognizing the constancy in culture of small differences of leaf form, independent of time of sowing, soil and weather conditions, etc., broadly divides the species into two main leaf-shape varieties:

(1) var. *lacerus* Wallr. (1822) = *Sonchus lacerus* Willd. (1800) (leaves pinnate, terminal lobe lanceolate, similar to lateral lobes).

(2) var. *triangularis* Wallr. (1822) = var. *lyratifolius* Beckh. = var. *runcinatus* Koch (1843–5) (leaves with terminal lobe much larger than lateral lobes, obtusely triangular). Zenari retains Willdenov's name for the first variety, which she regards as a subspecies, and refers to the second as *S. ciliatus* Lam. (1778) (excl. β). To these she adds a third 'subspecies', *S. subbipinnatifidus* (Guss.) Zen. n.comb. = *S. ciliatus* c. *subbipinnatifidus* Guss. (1854) = *S. α laevis* d. *subbipinnatifidus* Fiori (1904): it is described as having

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* Cf. *Crepis capillaris*, in which absence of glandular hairs on the involucre is controlled by a single (recessive) gene 'bald' (Collins, 1924).

'cauline leaves with distinct lobes, long, narrow, acuminato-falcate, with margin some-what deeply incised, especially above'.*

Ostenfeld includes a flower-colour variety, var. *albescens* Neum. (1889) (= var. *purpurascens* Druce = var. *lilacina* Beckh., since, in the absence of carotenoid from the florets, the anthocyanin on the dorsal surfaces becomes evident). Zenari points out two floret-colour varieties which are common in Italy, Britain, and probably elsewhere, though they are distinguished by few authors (e.g. Béguinot):

(1) var. *typicus*—primrose yellow (601/2 in Wilson, 1938, *H.C.C.* p. 65).

(2) var. *flavus*—aureolin 3 (*H.C.C.* p. 3).

I. *Geographical and altitudinal distribution. S. oleraceus* is an extremely common weed throughout England and Wales, occurring wherever soil is newly turned or rubble freshly deposited. It is found abundantly along roadsides, appearing more commonly than *S. asper* around human habitations. In Scotland it is distinctly the less common of the two annual species, but it is found in every vice-county of the mainland, as well as occasionally in the Hebrides, and Orkneys. A noticeable, but as yet unaccountable, absence of both species was observed in the Bradford district of Yorkshire (summer, 1943): further observations on this feature would be of interest. *S. oleraceus* ascends to a height of 1200 ft. in Yorkshire (*Alt. range Br. Pl.*): in the Alps (Cierfs) it reaches 1780 m. (Braun-Blanquet & Rübel, 1933); while a prostrate form is recorded as the highest Angiosperm on Mauna Kea, Hawaii, at 12,000 ft. (Rock, 1913).

II. *Habitat.* (a) *Climatic and topographical limitations. S. oleraceus* requires good illumination for full growth, and occasional specimens which survive in the shade of hedges are invariably emaciated and poorly grown. It is found in ploughed fields and waysides, wherever a fairly fertile open habitat presents itself, but not in undisturbed grassland or in woods, making an appearance only where new soil is exposed by rabbits, etc., or cleared by fire. Ridley (*Disp. plts.*) states that *S. oleraceus* is almost the only plant (except for *Carduus pycnocephalus*) on the bare patches around burnt gorse-bushes on the Dorset Downs, while bombed sites in many of our cities testify to its ubiquity (vide III below). It abounds in town gardens, building sites (Shenstone, 1912), on walls, and along roadsides, especially where ditching or burning exposes bare soil. Buchli (1936) records the occurrence of *Sonchus oleraceus* in thirteen out of 272 arable fields examined in north-east Switzerland (cf. *S. asper*).

Shade appears to be the chief factor excluding the species from closed communities: preliminary experiments have indicated that plants do not survive beyond the seedling stage if they are shaded to any great extent. Furthermore, the species seems to react to seasonal variation of illumination in the same way as do *Lactuca* spp. (Bremer & Grana, 1935) and *Tragopogon dubius* (Allard, 1942), in that short days tend to produce a rosette form of the plant, while a flowering stalk is only formed under conditions of longer hours of daylight. Therefore, seeds germinating in the autumn give rise to plants with the acaulescent habit of *Taraxacum officinale*, capable of withstanding a mild winter and producing an exuberant growth (Béguinot) and early flowers in the following year. *Sonchus oleraceus* is thus (at least in England) a 'winter annual'—a facultative therophyte

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* Both authors agree that *Sonchus oleraceus* v. *integrifolius* Wallr. (1822) was probably described from a depauperate specimen of the var. *triangularis* Wallr., of which the lower, more typically divided leaves were missing. This is very probably true: the illustration given by Hegi (*Fl.* 6, 2), purporting to represent this variety, appears to depict a plant of *S. asper*.

or biennial rosette hemicryptophyte. This elasticity of life cycle must contribute in large measure to the success of the species as a weed.

As in *Lactuca* sp. (Thompson, 1943), insolation, acting on the hereditary constitution of the plant, may stimulate the production of anthocyanin (apparently a cyanin 3-glycoside) in the leaves and stem. Specimens growing by a hedge have usually green stems and midribs, whereas in an open field even the leaf-laminae may be deeply pigmented, most noticeably on winter rosettes.

In moist weather, especially towards the end of the flowering season, the capitula are particularly prone to attack by *Botrytis cinerea*, which effectively sterilizes the flower-heads. The fruit-dispersal mechanism is intimately bound up with atmospheric humidity (vide VIII below).

The plants withstand considerable wind velocities on the exposed coasts of the Scilly Islands, etc., where conditions of high wind are frequent. The mechanical structure of the stem—a hollow cylinder with transverse internal septa, buttressed by five longitudinal ridges decurrent from the leaf midribs—is well adapted to withstand the stress of bending.

(*b*) *Substratum.* The species is far from exacting in its soil preferences, growing well especially on clay-rich, sandy, or loamy soils. It is absent from acid peat. Buchli (1936) records it from soils over a pH range of 6·5–9 (with a possible optimum at 8–8·5), and over ranges of 'Bodenskelett' (soil fraction of particles exceeding 2 mm. in diameter) from 0 to 62·5%, and of free $CaCO_3$ from 0 to 55%. In fact, flourishing plants are found on the bare sides of chalk-pits (e.g. at Dunstable, Bedfordshire, at a pH of 7·5*), where the absence of humus is evident. The statement by Hegi that the species is nitrophilous seems to lack substantiation. Hepburn (1942) records *Sonchus oleraceus* from a limestone community subject to periodical burning at Barnack, Northamptonshire (pH at surface, 7·2; below surface, 7·5). It is tolerant of saline conditions: plants not infrequently occur close above the drift line on the coast, and are found in the muddy sides of salt springs, e.g. in Cheshire. *S. oleraceus* is recorded along the shores of Ondaga Lake, Syracuse, N.Y., in a saline area with a soil chloride content of 660 p.p.m. and a pH of 8·1 (Young, 1936); it also was one of the earliest plants to colonize completely new terrain raised from the sea in Hawkes Bay, New Zealand, by the earthquake of 1931 (Oliver, 1942) and to appear as seedlings after the Norfolk sea floods of 1938 (Ellis, 1938).

III. *Communities.* *S. oleraceus* exhibits such a wide range of tolerance of soil conditions that it may be found associated with any other weeds of arable land. Long (1938) lists an association of weeds in a garden plot in May. The following tables illustrate the wide range of plants with which this species may be associated in three somewhat characteristic habitats: frequency symbols have been omitted since the lists were compiled by different observers at different times, and because such symbols appear of doubtful value when applied to an open community (cf. Hope-Simpson, 1940).

IV. *Response to biotic factors.* Bare soil exposed by rabbits or moles, and communities opened by burning, felling, or many other of man's activities, usually offer favourable conditions for the growth of the species; it tends to disappear, largely as a result of shading, as the community becomes 'closed'.

Despite its bitter taste (the latex contains considerable quantities of catechol), the plant is eaten by rabbits and other herbivores, although not preferentially. It can withstand little trampling, but a specimen crushed or broken down in its early stages

* Glass electrode and Cambridge potentiometer: det. G. E. Fogg.

frequently recovers to send up a ring of branches from the base of the broken main stem. Regeneration apparently cannot take place from the tap root.

V. (a) *Gregariousness*. In open ground the frequency of individuals depends mainly on the supply of fruits. Soil which has borne this species in previous seasons may produce

Table 1. *Pioneer communities of bare chalk*

A, Harefield, Middlesex. Home-guard range, cleared 1940: plants listed 1943 (Locket, 1946).
B, War Down, Hampshire. Chalk quarry, spoil bank talus, southern aspect (Tansley & Adamson, 1925).
C, Sewell, Bedfordshire. Chalk quarry, spoil bank (December 1942, R.A.L.).
D, Dunstable, Bedfordshire. Chalk quarry, spoil bank (September 1946, R.A.L.).

	A	B	C	D		A	B	C	D
Achillea millefolium	+	−	−	+	Lotus corniculatus	+	+	−	+
Agrostis stolonifera	+	+	+	+	Medicago lupulina	+	−	+	−
Anthoxanthum odoratum	−	+	−	−	Onobrychis viciifolia	−	−	+	−
Anthyllis vulneraria	−	−	+	−	Papaver rhoeas	−	−	+	−
Arrhenatherum elatius	+	−	+	+	Phleum pratense	−	−	+	+
Artemisia vulgaris	+	−	−	−	Picris hieracioides	−	−	+	−
Asperula cynanchica	−	+	−	−	Pimpinella saxifraga	+	−	−	+
Betula pendula	+	−	−	−	Plantago lanceolata	−	−	+	−
Bromus erectus	+	−	−	−	P. media	+	−	−	−
Carex flacca	−	+	−	−	Poa compressa	−	−	+	−
Carlina vulgaris	−	+	−	−	Populus sp.	+	−	−	−
Centaurea nigra	+	−	+	−	Poterium sanguisorba	−	−	+	+
Chamaenerion angustifolium	+	−	−	+	Prunella vulgaris	−	−	+	−
Chrysanthemum leucanthemum	+	−	−	−	Pyrus sp.	−	−	+	−
Cirsium acaulon	−	+	−	−	Ranunculus bulbosus	+	−	+	−
C. palustre	−	+	−	−	Reseda lutea	−	−	+	+
C. vulgare	+	−	+	−	R. luteola (1941)	(+)	−	−	−
Clematis vitalba	+	+	+	−	Rosa canina agg.	+	−	+	−
Convolvulus arvensis	−	−	+	−	Rubus fruticosus agg.	+	−	+	−
Crataegus monogyna	−	−	+	−	Rumex acetosa	+	−	−	−
Crepis biennis	+	−	−	−	R. crispus	+	−	−	−
C. capillaris	−	−	−	+	Salix atrocinerea	+	−	−	−
C. taraxacifolia	+	−	+	+	S. caprea	+	−	−	−
Dactylis glomerata	+	+	+	−	Scleropoa rigida	−	−	−	+
Daucus carota	+	−	+	+	Scrophularia nodosa	+	−	−	−
Diplotaxis muralis	−	−	+	−	Senecio erucifolius	+	−	+	−
Echium vulgare	−	+	−	−	S. jacobaea	−	−	+	+
Epilobium montanum	−	−	−	+	S. vulgaris	−	−	+	+
Euphrasia officinalis agg.	−	+	−	−	Silene cucubalus	−	−	+	+
Festuca ovina and F. rubra	+	+	+	+	Sinapis arvensis	−	−	+	+
F. pratensis	−	−	+	−	Solanum dulcamara	−	−	+	−
Galium mollugo	−	−	−	+	Sonchus arvensis	−	−	−	+
Gentiana amarella agg.	−	+	−	−	S. asper	−	−	+	+
Heliototrichon pratense	−	+	−	−	S. oleraceus	+	+	+	+
H. pubescens	+	−	−	−	Taraxacum laevigatum	−	+	−	−
Heracleum sphondylium	+	−	+	−	T. officinale	+	+	+	+
Hieracium pilosella agg.	+	+	+	−	Thymus serpyllum agg.	−	+	−	−
Hypericum perforatum	+	−	−	−	Trifolium pratense	+	−	+	+
Knautia arvensis	−	−	+	−	T. repens	−	−	+	−
Lathyrus montanus	−	−	+	−	Tussilago farfara	+	+	+	+
Leontodon autumnalis	−	−	+	+	Veronica chamaedrys	+	−	+	+
L. hispidus	+	+	−	+	Vicia sativa	+	−	−	−
Linaria minor	−	−	−	+					
Linum catharticum	−	+	+	+	**Totals**	**42**	**23**	**48**	**31**
Lolium perenne	−	−	+	−					

Bryophytes A, Bryum capillare, Barbula fallax. B, Camptothecium lutescens, Hypnum chrysophyllum, H. molluscum, Neckera complanata. D, Dicranella varia. (Seligeria calcarea and Tortula muralis on larger boulders broken from cliffs.)

a thick crop when newly turned, but the best-grown plants are those standing some distance from a neighbour. The similarity in variable genetic factors which is exhibited by specimens within a single clump of plants is indicative of common parental origin.

(b) *Performance in various habitats.* See V (c), VI (c) and VIII (c).

(c) *Effects of light, frost and drought.* In good light and loose bare soil, or by ditches, large, profusely branched specimens up to 6 ft. (1·8 m.) in height may be produced: the usual height is only half of this, however. Etiolated plants, with pale flaccid leaves and long slender internodes, may occasionally be found in hedges: Gardiner (1848) records a specimen 9–10 ft. high (2·7–3 m.), supported in a hawthorn hedge.

Table 2. *Weeds of bombed sites in London*

E, Temple: August 1943.   F, Fetter Lane: August 1943.

	E	F		E	F
Acer pseudoplatanus	+	–	Papaver rhoeas	+	–
Achillea millefolium	–	+	Phalaris canariensis	+	–
Aethusa cynapium	+	–	Plantago media	–	+
Agrostis tenuis	+	–	Poa annua	+	–
Artemisia vulgaris	+	–	P. pratensis agg.	+	+
Ballota nigra	+	–	Polygonum aviculare agg.	+	+
Calystegia sepium	–	+	P. persicaria	+	+
Carex sp.	+	–	P. sieboldii	–	+
Chamaenerion angustifolium	+	+	Ranunculus repens	+	–
Chenopodium album	+	+	Senecio sylvaticus	+	+
Chrysanthemum parthenium	+	–	S. vulgaris	+	–
Cirsium arvense	+	–	Solanum nigrum	+	–
C. vulgare	–	+	Sonchus arvensis	+	–
Erigeron canadense	+	+	S. oleraceus	+	+
Euphorbia peplus	+	–	Stellaria media	+	–
Fagopyrum sagittatum	+	–	Taraxacum officinale	+	–
Fraxinus excelsior	+	–	Trifolium repens	+	–
Galinsoga parviflora	+	–	Tussilago farfara	+	–
Lactuca serriola	+	–	Urtica dioica	+	–
Lolium perenne	+	–	Vicia hirsuta	+	–
Lotus corniculatus	+	–			
Matricaria matricarioides	–	+	Totals	36	15
Oenothera stricta (?)	–	+			

Table 3. *Flora of maritime cliffs*

G, Slope of approx. 30°, Guernsey, Channel Islands: June 1946.

Agrostis tenuis
Aira caryophyllea
A. praecox
Alchemilla arvensis
Anagallis arvensis
Anthoxanthum odoratum
Chrysanthemum leucanthemum
Dactylis glomerata
Erodium cicutarium agg.
Festuca ovina
Filago minima
Hieracium pilosella agg.
Holcus lanatus
Hypochoeris glabra
Jasione montana
Lotus angustissimus
Matricaria chamomilla
Ornithopus perpusillus (?)
Plantago coronopus

P. lanceolata
Rumex acetosella
Sarothamnus scoparius
Scilla autumnalis
Sedum anglicum
Senecio jacobaea
S. sylvaticus
Silene maritima
Sonchus oleraceus
Teesdalia nudicaulis
Teucrium scorodonium
Thymus serpyllum agg.
Umbilicus pendulinus
Vulpia bromoides

Pteridium aquilinum

Polytrichum piliferum
(Lichens)

Total (Angiosperms)   33

Winter rosettes are certainly capable of withstanding temperatures of several degrees below freezing-point without sustaining injury, but the flower-buds are killed by early winter frosts. About mid-November, in the south and midlands, the proportion of

fertile achenes falls, and after 2 or 3 weeks of sterile flowering the heads wither, and necrosis advances down the stem. Scully (1916) records that in Co. Kerry flowers may be found at all times of the year: this appears to be the case also in the Scilly Isles.

The plants can survive short periods of drought sufficiently severe to cause wilting of the leaves.

VI. (a) *Morphology of underground parts*. There is usually a single tap-root, from which thin laterals radiate more or less superficially: the details appear not to differ from those of *S. asper* (q.v.). The tap-roots of plants growing in crevices in quarries, etc., may be long and wiry; while those of winter rosettes tend to be stout and woody.*

(b) *Mycorrhiza*. There is no evidence of mycorrhiza. (An endotrophic fungus has been reported in the roots of *S. arvensis* by McDougall & Glasgow (1929).)

(c) *Perennation; reproduction*. There is no vegetative reproduction: seasons unfavourable to growth—winter in temperate climes, and summer in the tropics (Ostenfeld, 1917)—are tided over by the 'seed'. In addition, seedlings which germinate in the autumn produce a rosette of radical leaves (cf. Johnston, 1853) which is capable of surviving the winter, and of sending up a flowering stem in the following spring.

In conditions favourable to flowering, such as impoverished soil and warm weather, capitula may be produced within 6 weeks of germination. There may thus be more than one generation per annum (Jordan, 1847). Flowers are produced in the first or second season, depending on time of germination, but in no case does the individual survive after a single flowering season.

(d) *Chromosome number*. Diploid chromosome numbers have been ascertained as follows: Belgium: 16 (?) (Marchal, 1920). Japan, U.S.A., Great Britain: 32 (Ishikawa, 1916; Cooper & Mahoney, 1935; Barber, 1941; Rutland, 1941; R.A.L.).

(e) *Physiological data*. No information.

VII. *Phenology*. Specimens which have survived the winter in the rosette form commence to produce a flowering stem about the middle of March, and to flower at the end of April: seedlings germinating in the middle of March are rarely found in flower before the beginning of June. In the south and Midlands, flowering continues until about mid-December, but on the Atlantic seaboard some flowers may be found at all seasons if the weather is sufficiently mild. Achenes are produced abundantly between May and November, and in suitable conditions will germinate in light or darkness within 2 days. No 'frost period' is necessary.

The periods required for maturation of achenes vary with the time of year and with local weather conditions. In late autumn, flower-heads may remain open for over a week, and after a period of cool, moist, overcast weather no 'seed' is set. Times observed in spring and summer are given below.

Table 4. *Time in days after initial opening of involucres of* S. oleraceus

	Ledbury, Herefordshire (24 April 1944)	John o'Groats, Caithness (20 August 1942)
Outer florets open	1	1
All florets open	2	2
Dispersal of mature achenes	20	9

* Warming *et al.* (1909, 1933) refers to '*S. oleraceus*' as spreading by creeping roots and suckers. Possibly *S. arvensis* is referred to.

VIII. (a) *Floral Biology*.* It is probable that in nature most of the achenes are self-fertilized, since there is rarely much variation among the progeny of plants exposed to open pollination. The flowers are self-fertile as in *Lactuca* sp. (Durst, 1930), fertilization taking place within a few hours of pollination. Also, as in *Lactuca* (Thompson, 1938), the period in the day during which pollination can take place is short: on a sunny morning, following a warm night, the flower-heads open earlier, and remain open for a shorter period, than under cool or overcast conditions. Capitula which have not previously flowered tend to open 1 or 2 hr. later than those which have already opened on the preceding day: the process of opening may take 2 hr., that of closing often less than 1 hr. The following times have been observed during fine spells:

Table 5. *Time of day when capitula of* S. oleraceus *are open*

Locality	Uppsala	Innsbruck	John o'Groats
Observer	(Linnaeus)	(Kerner)	(R.A.L.)
Season	?	June–July	August
Ref.	Knuth, Poll.	Knuth, Poll.	—
Open	5 a.m.	6–7 a.m.	7–9 a.m.
Closed	11 a.m.—noon	1–2 p.m.	Noon—1 p.m.

No cleistogamic flowers are produced, and there is no evidence for apomixis (Barber, 1941). Removal of the styles before anthesis results in complete sterility of the ovules.

Many species of syrphids visit the flowers for nectar, and throughout the summer numbers of the small beetle *Meligethes aeneas* may be found on the flowers of *Sonchus* sp. and other yellow Composites, feeding on the pollen. (It may be of interest to record that a single flower-head of *S. oleraceus* may produce up to 100,000 pollen grains.)

A list is appended of some of the insect visitors which have been recorded: it has not been considered practicable for this purpose to distinguish *S. asper* from *S. oleraceus*. The list has been compiled from Drabble & Drabble (1917), Knuth, Poll., Müller (1883), Scott-Elliot (1896), and from information kindly supplied by Dr G. D. Morison, Dr O. W. Richards and the Rev. C. E. Tottenham.

HEMIPTERA

ANTHOCORIDAE: *Orius majusculus* (Reut.).

THYSANOPTERA

Taeniothrips atratus (Hal.), *T. vulgatissimus* (Hal.), *Thrips flavus* Schrank, *T. tabaci* Lind.

LEPIDOPTERA

PIERIDAE: *Pieris brassicae* L.

COLEOPTERA

NITIDULIDAE: *Meligethes aeneas* (Fab.).

HYMENOPTERA

APIDAE: *Andrena fulvago* (Christ.), *Bombus lapidarius* (L.), *Chelostoma campanularum* (L.), *Coelioxys rufescens* (Lep.), *Dasypoda hirtipes* (F.), *Halictus leucopus* (Kby.), *H. leucozonius* (Kby.), *H. morio* (F.), *H. smeathmanellus* (K.), *H. villosus* (K.), *Stelis aterrima* (Pz.).

SPHECIDAE: *Diodontus luperus* (Shuck.).

* For general features, vide Small, 1919.

DIPTERA   •

MUSCIDAE: *Egle radicum* (L.), *Morellia hortorum* (Fall.).

SCATOPSIDAE: *Aldrovandiella coxendix* (Verr.).

SYRPHIDAE: *Eristalis arbustorum* (L.), *Melanostoma mellinum* (L.), *Platychirus albimanus* (F.), *P. clypeatus* (Mg.), *P. manicatus* (Mg.), *Syrphus arcuatus* (Fall.), *S. balteatus* (Deg.), *S. rubesii* (L.).

TACHINIDAE: *Bucentes geniculata* (Deg.).

(b) *Hybrids.* It appears unlikely that many of the 'hybrids' between *Sonchus oleraceus* and *S. asper*, which are reported from time to time, are in fact of mixed descent: the term tends to have been used 'as a label for misfits' (Darlington, 1937). Herbarium specimens which have been examined usually lack definite evidence of hybrid origin, and fall within the range of form of one or other of the putative 'parent' species, as far as could be judged from the dried material. Zenari (1921) states that she was unable to find any hybrid plants, despite the frequent association of the two species in nature.

Barber (1941) describes an undoubted hybrid which arose spontaneously in cultivation: the chromosome number proved to be 25 (*S. oleraceus*, $2n = 32$: *S. asper*, $2n = 18$), and the plant was sterile both in pollen and ovule. It was characterized by a single long tooth on the otherwise rounded auricles, and by leaves intermediate in character between those of the parents. A specimen with these vegetative characters, with immature achenes (possibly of the *S. asper* type), was found in Cambridge in 1941. Another large plant of the same nature, completely sterile, was discovered in a railway siding at Kinnersley, Shropshire, in 1943. Unfortunately, circumstances did not permit of cytogenetical confirmation of the hybrid origin. Barber (loc. cit.) was unable artificially to repeat the hybridization, and there can be little doubt that hybrids are extremely rare, at least in Europe. Other records for Great Britain (with the above *caveat*) include those of Bennett (1890) from Dumbarton; of Druce (1917) from Wilsford Manor, Wiltshire (apparently *S. oleraceus*), and (1923) from Rozel, Jersey ('*S. Picquetii*'—probably also *S. oleraceus*); and of Harrison (1944) from Island of Rhum, North Ebudes.

However, Kirk (1893) states that '...it is certain that seeds of both forms must have been repeatedly introduced (into New Zealand)...and that cross-fertilization has taken place, since fruits of the typical form exhibit all degrees of murication...'. A genetical analysis of the species in New Zealand would be of great interest.

(c) *Seed production and dispersal.* The number of flower-heads per plant may vary from a single one, in extremely depauperate plants, to many hundreds. A very well-grown specimen from a garden (Cambridge, 15 August 1945) bore the following numbers of capitula (the main stem was about 5 ft. high (1·5 m.), but several of the lateral branches were missing, so that the figures given are under-estimates):

Table 6. *Numbers of capitula on a large plant of* S. oleraceus

Flower-buds exceeding 1 mm. in diameter	612
Capitula in the process of flowering	46
Capitula containing ripening fruits	335
Empty capitula, the fruit having dispersed	614
Total	1607

Variation under different conditions—size of plant, depending on soil fertility and time of year, etc.—is so great that it is difficult to give even an approximate estimate of the

average number of fruits produced per plant. Possibly 10,000 is a fair figure for a season: the range extends from 200 to 200,000. Salisbury (*Rep. Capac.*) gives 140 as an average number of achenes per capitulum, and 43·7 as the average number of capitula per plant (based on 65 plants examined)—i.e. over 6000 fruits per plant. The ripe achenes are dispersed mainly by wind. At least three separate hygroscopic mechanisms contribute to the efficiency of the process:

(1) The pappus, which is formed early in the development of the floret, is composed of two types of hairs. Those of the inner ring are longer and more rigid than those of the outer, and are set with acropetally directed spines. At the end of flowering, the corollae wither and, in drying, shrink; but as the spines of the pappus prevent their shrivelling in a downward direction, they become detached from the apex of the ovary and 'work their way' upwards. From 3 to 6 days after the end of flowering, the remains of the corollae fall in a dry tuft from the apex of the conical fruiting involucre. (Cf. several British species of *Senecio*, in which the fruits on dispersal remain encumbered with remains of the corolla.)

(2) The inner surface of the involucral bracts is faced with a glossy layer of rigid cells with thickened walls. While the outer layers remain turgid, the involucre is held closed, but when the fruits are ripe these outer cells lose turgor during a dry spell, and their shrinkage causes the involucre to open, freeing the achenes and pappuses for wind dispersal. In dry conditions the involucral bracts may become adpressed to the peduncle, while under high atmospheric humidity the involucre closes: such hygroscopic movements may continue for a day or two after the dispersal of the achenes. (Cf. *Senecio vulgaris*, in which the same, probably widespread, phenomenon has been described.)

(3) At the distal end of the achene, below the insertion of the pappus, is a zone of thin-walled cells. On exposure to dry air, these cells shrink, causing the pappus tuft to splay out from the original erect position, and thus increasing its efficiency for wind dispersal. (This zone of cells is visible to the naked eye in *Tragopogon pratensis*. The feature has been described for *Sonchus palustris*, inter alia, by Hirsch (1901).)

Dallman (1933) gives the achene weight of *S. oleraceus* as 0·00042 g. Praeger (1911) found that achene-bearing pappuses fell through 12 ft. of still air in 12·7 sec., and it is certain that airborne fruits are responsible for the rapid appearance of *Sonchus* spp. on newly opened habitats such as bombed sites (Salisbury, 1943).

Since *S. oleraceus* frequents the banks of streams, etc., dispersal of achenes by water may contribute to its spread. The fruits float for 3 days or more (Praeger, 1911).

Pappus hairs of the outer zone are shorter and thinner than those of the inner. They are flexuous and equipped with terminal hamuli, tending to cling to clothing, wool, etc. (Stebbins, 1940). In addition, the achenes bear hooked teeth along the margins and the lateral ribs. These features may contribute somewhat to the dispersal of the fruits.

Achenes occur as contaminants in seed samples, thereby furthering their distribution as arable weeds. They have been found with seed of clover and lucerne (Gentner, 1929), with oats and Italian rye-grass (Praeger, 1911), etc.

Several species of finch, skylarks, etc., feed on the achenes (Collinge, 1913), while partridges occasionally take whole capitula (Middleton & Chitty, 1937). Collinge was able to raise seedlings of *S. oleraceus* from the droppings of bullfinches (*Pyrrhula* sp.), so that it appears that dispersal may also be assisted by birds and other animals through the faeces.

(d) *Viability of seeds; germination.* Unfertilized ovaries produce small, thin, white achenes, which are readily distinguished from fertile fruits. Throughout the summer their number is small, but the proportion rises at the end of the season until no good fruit is set. From fertile achenes 100% germination may be obtained on wet filter-paper (Gill, 1938). Gill also states that achenes ripen successfully on plants which have been cut down, provided that the flowers were already open at the time of cutting. This is of some practical importance.

Ewart (1908) was unable to obtain germination in samples of 300 and 150 achenes of *Sonchus oleraceus* gathered respectively 17 and 50 years previously. (He quotes, however, some doubtful records by Peter (1894) in which 'a few' achenes of this species germinated after storage for (?) 100 years.) Ewart's observations are in agreement with data given by Dorph-Peterson (1924), quoted herewith (Table 7):

Table 7. *Germination of achenes collected in 1904 (percentages)*

Year of sowing	1905	1906	1907	1908	1909	1910	1911	1912	1913	1914	1915	1916	1917	1918
Unripe when collected	62	50	47	43	61	33	48	35	21	25	1	0	0	0
Ripe when collected	87	64	53	49	59	56	33	30	19	8	1	0	0	0

It appears that the achenes remain viable for about 10 years: but it is not clear why these figures are so low throughout.

Chippindale & Milton (1934) raised seedlings of *S. oleraceus* from soil taken at depths down to 10 in. on land which had not been ploughed for 50 years, and at a depth of 2–3 in. on natural marsh grassland for which there was no record of cultivation. If these plants did not grow from subsequent wind-borne 'intruders' (cf. Brenchley, 1918) it is probable that the fruits had been buried by the activities of earth-worms or other agencies; and it is doubtful whether, even in the former case, they had remained from the original period of cultivation.

(e) *Seedling morphology.* Seedlings of *S. oleraceus* can readily be distinguished from those of *S. asper* by the more cordate form of the young leaves, the lamina being more abruptly decurrent and the petiolar wing narrower. They are illustrated by Long (1929), see Fig. 2.

Fig 2. Seeding of *S. oleraceus*, 2 weeks old (× 2). (Note sudden contraction of lamina into petiole.)

(f) *Effective reproduction* is by seed only.

IX. (a) *Animal parasites or feeders.* The following list of animal parasites has been kindly prepared by Dr O. W. Richards, in conjunction with Dr H. F. Barnes, Mr R. B. Benson, Mr C. T. Gimingham, Dr A. M. Massee and Dr J. Smart.

Insects. It has not proved practicable to distinguish between the two species, but the following British records refer to insects found feeding on annual species of *Sonchus* except where the contrary is indicated.

HOMOPTERA

APHIDIDAE: *Macrosiphum sonchi* (L.), *Amphorophora cosmopolitana* Mason, *Myzus lactucae* (Schrank), *Aphis compositellae* Theob., *Trama troglodytes* Heyden (roots), *Pemphigus bursarius* (L.).

DIPTERA

CECIDOMYIDAE: *Cystiphora sonchi* (F. Löw.) (pustules on leaves), *Contarinia schlechtendaliana* Rübs. = *C. sonchi* Kieff. (swollen flower-heads).

MUSCIDAE: *Myopina reflexa* R.D. (leaf miner).

TRYPETIDAE: *Trypanea amoena* (Fzfld.), *Ensina sonchi* (L.), *Tephritis formosa* Lw. (*T. dilacerata* Lw., and *Paroxyna tesselata* (Lw.) (on *S. arvensis*) (all forming galls in the capitula).

AGROMYZIDAE: *Melanagromyza pulicaris* (Mg.) (leaf miner), *Phytomyza atricornis* Mg. (leaf miner, often very abundant: highly parasitized by an unidentified hymenopteran), *P. lateralis* Fall. (galls at base of stem).

LEPIDOPTERA

NOCTUIDAE: *Polia advena* (Schiff.), *Cucullia umbratica* (L.), *C. lactucae* (Schiff.), *Hadena serena* (Fab.) (on flowers), *H. dysodea* (Hb.) (on flowers).

OECOPHORIDAE (*Tortricidae*): *Depressaria badiella* (Hb.). (*Eucosma expallidana* (Haw.) and *Argyroploce purpurana* (Haw.) on flowers and roots respectively of *S. arvensis*.)

HYMENOPTERA

CYNIPIDAE: *Timaspis sonchi* Stef. (galls in stems).

Other animals

ACARINA

PHYTOPTIDAE: *Phytoptus sonchi* (Nal.) (swellings on leaves).

NEMATODA

Tylenchus devastatrix.

(b) *Plant parasites.* (Data kindly supplied by Dr A. Smith.) Few fungi appear to have been recorded in the British Isles on *Sonchus oleraceus* and *S. asper*:

PHYCOMYCETES

PERONOSPORALES: *Bremia lactucae* Regel (common on both species).

FUNGI IMPERFECTI

COELOMYCETES: *Ascochyta sonchi* Grove (*S. oleraceus*).

HYPHOMYCETES: *Botrytis cinerea* Fr. (no published record but sometimes causes damage to capitula, especially at the end of a wet season such as 1946).

ASCOMYCETES

ERYSIPHALES: *Erysiphe cichoriacearum* DC. (common on both species).

BASIDIOMYCETES

UREDINALES: *Puccinia sonchi* Rob., *Coleosporium sonchi* Lev. (both common on both species).

Of the four fungi mentioned as being common on both species, the last three are favoured by hot dry weather and it is difficult to disentangle the effect of the fungus from that of the drought. Though conspicuous they seldom seem to harm the plant more than slightly. *Puccinia sonchi* seldom produces teleutospores, but does so more readily in hot summers. They may also be induced by transplanting the host. Some plants produce normal two-celled spores while others produce nothing but single-celled ones (mesospores).

Aphids (*Amphorophora lactucae*) on *Sonchus oleraceus* at Hauxton, Cambs. (19 May 1946) were heavily infected with a fungus which might under some circumstances have some material effect in their control. The spores were ovate, $26 \times 15\,\mu$ and with the assistance of Dr Alan Burges the species was identified, tentatively, as *Empusa Fresenii* (sp. ovate, $20 \times 17\,\mu$).

BACTERIA: artificial infection by *Bacterium tabacum* has been recorded by Johnson, Shagg & Murwin (1924).

(c) *Diseases*. No clear records of virus infection have been found. Brandenburg (1929) reports mosaic-like symptoms on *Sonchus oleraceus*. Specimens collected in Cambridge in 1946 exhibited a vein-clearing pattern on the leaves (cf. similar symptoms described by McCrea (1922) for a plant of *S. asper*): they were kindly investigated by Dr K. M. Smith, but no virus infection was detected. Local lesions may be artificially produced by Tobacco Necrosis virus (Smith, 1937), while Kunkel (1926) has experimentally transferred the virus of Aster Yellows to *S. oleraceus* and thence back to *Aster*. The symptoms he describes include stunting and chlorosis with some vein-clearing and reduction of leaf serration.

X. *History*. It is suggested (Dunn, 1905) that *Sonchus oleraceus* is native to wet sandy places round the Mediterranean Sea, but, though probably Eurasian in origin, one cannot be certain that the species is truly indigenous in this country. A natural habitat is found, however, in open communities round the shores, notably in the Channel Isles, Devon (Martin & Fraser, 1939), etc., where it may be native to the sea cliffs.

Despite the fact that the fruits preserve well and abundantly in more modern deposits, no records of *S. oleraceus* have been found in British pre-glacial beds (Reid & Reid, 1908), though remains have been found in Silchester (Hants.) from Roman period I (Reid, 1901).

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Sonchus asper (L.) Hill*

S. asper is in most respects similar to *S. oleraceus*, but differs considerably in the leaf form. The margins of the laminae are often crisped and spinous, and the upper surface of such leaves is usually of a dark, glossy green. In the variety *inermis*, the margins are almost plane, and more or less regularly set with soft spines, while the surface is frequently somewhat glaucous, and the stems and midribs are usually purplish (cf. *S. asper* var. *cruentus* Murr., 1902). Intermediate forms, however, occur. The lower leaves, unlike

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* *S. oleraceus* γ et δ *asper* L. (1753); *S. asper* Hill (1769), Herb. Brit., 47.
Note that *S. asper* Gaertn., Mey. & Scherb. = *S. oleraceus*; and that *S. asper* Wulf. = *Picris hieracioides*.
The species is well illustrated by Borrer (1834).

those of *S. oleraceus*, do not show a clear distinction between petiole and lamina, and the auricles are always rounded and adpressed. The leaves are rarely runcinate-pinnatifid, but in such cases the terminal lobe is less wide than the penultimate pair, whereas in *S. oleraceus* it is usually the widest. The achenes provide one of the clearest criteria of distinction between the two species.

Fig. 3. *Sonchus asper* (L.) Hill. Vice-comital distribution in the British Isles and (inset) distribution in Europe.

KEY. Broken line: limit of isolated records. Continuous line: limit, south of which plant is relatively common.

The achenes of *S. asper* are smooth, obovate, approximately 2·5 mm. in length and usually 1 mm. in width: in Scotland a winged form of achene up to 1·5 mm. broad is common. Achenes of *S. oleraceus* are rugose, truncate, oblanceolate, 3 mm. in length and about 0·75 mm. in breadth, and are invariably devoid of a 'wing'. According to Zenari (1921), who illustrates transverse sections of the achenes of both species, those of *S. oleraceus* also differ from *S. asper* achenes in the presence of a furrow flanking the three longitudinal ridges. In *S. asper*, recurved hooks on the achene are confined to the margin of the wing, whereas in *S. oleraceus* they also occur along the ribs. Ridley (*Disp.*

Plts.) attributes to this feature the wider range of the latter species among the islands of the Pacific, etc.; but this appears an improbable reason for the difference in distribution.

The achenes of *S. asper*, in their complete lack of transverse ridges, are quite distinct from those of any other European species (Béguinot), except for *S. glaucescens* Jord. (not a native of Britain), which Zenari (1924), following Fiori (1904), includes in the 'cycle' of *S. asper*. In this country there can therefore be no difficulty in distinguishing the two species by the characters of the mature achenes alone (Bronfield, 1861; Little, 1932—but cf. Kirk, 1893). In addition, the auricles of the *upper* leaves of *S. oleraceus* are sagittate, whereas those of *S. asper* are rounded and adpressed: and in the latter the upper bract-leaves and auricles are set with spines. The leaves of *S. oleraceus* never have the dark green, glossy appearance of *S. asper* var. *pungens*, nor the entire margin of *S. asper* var. *inermis*. If the seedling leaves have not died off, they provide a further diagnostic feature (vide Figs. 1 and 2). The florets of *S. asper* are less spreading than are those of *S. oleraceus*, and, perhaps invariably, golden yellow, whereas in *S. oleraceus* they vary in colour. In most floras no mention is made of this distinction between *S. oleraceus* and *S. asper*, though the fact that the flowers of the former species may be paler is mentioned by Druce (1886), Horwood (1919), and in a number of European floras (cf. Aschers. & Graebn.; Blytt, 1906; Lange, 1886–8; also Hultén, E. in litt.). The pappus of *S. asper* is more readily detached from the ripe fruits. The latex, on exposure to air, darkens to a deeper brown than does that of *S. oleraceus*. Both species possess vascular bundles within the stelar ring, but in *S. asper* they are more numerous, and often larger and more complex in structure (Zenari, 1924).

Biologically, however, this species differs in so few respects from the last that only remarks and observations applying specifically to *S. asper* are given below: in general, the description of the foregoing species applies equally well to both.

There is some evidence of ecotypic variation, but no detailed investigations have been carried out.

The habit, leaf form and degree of spininess, pigmentation, etc., are largely controlled by environmental factors such as time of sowing and degree of shading.

Ostenfeld (1917) recognizes two varieties:

(1) var. *inermis* Bisch. (1851) = var. *mollis* C. & G. (1845) = *S. fallax* α *laevis* Wallr. (1822). (Leaves all 'simple', obovate or lanceolate-ovate, obtuse; margin with small softish spines.)

(2) var. *pungens* Bisch. (1851) = var. *vulgaris* C. & G. (1845) = *S. fallax* β *asper* Wallr. (1822). (Lower leaves pinnatifid, acute; upper entire; margin crisped, with pungent spines.)

On the other hand, Zenari (1924), who also carried out a series of observations on plants kept under controlled conditions, considers that the variation between spiny and simple-margined forms is a function of the environment, and has described the extreme variants as α *typicus* and β *subintegrifolius* respectively. She recognizes four major 'subspecies' on various grounds: the first three of these may each exhibit variation of the type mentioned:

(1) *S. runcinatus* (Fiori) Zen. n.comb. = *S. oleraceus* β *asper* b. *runcinatus* Fiori (1904) = *S. asper* var. *elatior* C. & G. (1845). (Leaves lyrato-runcinate, segments oblong, teeth not pungent.)

(2) *S. spinosus* Lam. (1778) (excl. β) = *S. asper* β *pungens* Bisch. (1851). (Leaves more

laciniate, terminal lobe approximately equal to laterals, more rigid, with undulant spinose margin.)

(3) *S. viridis* Zen. (Whole plant lacking anthocyanin.)

(4) *S. decipiens* (DNtrs.) Zen. n.comb. = *S. asper* α *decipiens* DNtrs. (1843) = *S. asper* var. *pinnatifidus* Lojac. (1902) = *S. oleraceus* β *asper* d. *decipiens* Fiori (1904). (Leaves runcinato-pinnatipartite, segments recurved, linear oblong or angulo-dentate, more or less spinescent.)

A series of genetical experiments, carried out in controlled conditions over a number of years, is obviously needed before the variations of such a polymorphic species can be objectively described in terms of genes and environmental factors.

I. *Geographical and altitudinal distribution. S. asper* is among the commonest annual weeds of arable land, and is considerably more troublesome in most regions than *S. oleraceus*. Buchli (1936) records the occurrence of this species in 153 out of 272 arable fields examined in north-east Switzerland, where it shows a high correlation with winter cereal crops, especially wheat. It is the more common of the two species in Scotland, extending to the Hebrides and Orkneys, and as far as Unst in the Shetlands (Druce, 1920). Johnson (1925) records *S. asper* from a rubbish heap on the seashore at Stromness, and states that it is 'not native, rare, and sparingly in fruit'. This could certainly not have been said in 1942, which suggests that even within the last few decades the species has been extending its range. It ascends to a height of 1300 ft. in Yorkshire (*Alt. range Br. Pl.*) and to 1800 m. in the Alps (Engadin) (Hegi, *Fl.* **6**, 2).

II. *Habitat. S. asper* is recorded as a rare wind-blown adventive in damp oak-woods in the Midlands (Horwood & Noel, 1933). Watt (1940) records seedlings of this species from Breckland, on 'A'-type grassland (pH 8·0–8·5 at surface). Plants from this habitat may be as little as 15 cm. in height, producing only one or two capitula on an unbranched stem.

In the United States this species is recorded between storm-tide limits along the coastal salt-marshes of California (Purer, 1942) and Maryland (Pickering, 1879); Pickering also points to the frequent association of *S. asper* with salt-works in the Hawaiian Islands.

VI. (*a*) *Morphology.* Cole & Holch (1941) describe a well-grown specimen from rich soil: the stem was 4 ft. in height, and the maximum root-depth 27 in., while the spans of the aerial and underground systems were about equal. There is no significant difference in habit from *S. oleraceus*: a shade form, corresponding to *S. oleraceus* 'var. *gracilis*', and a winter rosette form (with leaves less divided and less spinous than those produced on the flowering stem of the typical variety) likewise occur. The latter is somewhat more resistant to frost than the corresponding form of *S. oleraceus*.

(*d*) *Chromosome number.* The diploid number has been ascertained for British specimens as 18 (Barber, 1941; Rutland, 1941; R.A.L.).

VIII. (*c*) *Seed production and dispersal.* A well-grown plant from Kinnerley, Shropshire (18 July 1943), was found to bear the following numbers of capitula. The main stem was 5 ft. in height, and one large branch was missing.

Table 8. *Numbers of capitula on a large plant of* S. asper

Flower-buds exceeding 1 mm. in diameter	817
Capitula in the process of flowering	60
Capitula containing ripening fruits	342
Empty capitula, the fruit having dispersed	367
Total	1586

Salisbury (*Rep. Capac.*) gives 105 as the average number of capitula on twenty-five plants examined, with 197·5 as an average number of achenes per capitulum. (A well-grown capitulum (Cambridge, 30 May 1946) contained 286 achenes, all but three fertile.) It does not appear that there is any appreciable difference in reproductive capacity between this species and the last.

The weight of the fruits (0·00030 g.—Dallman, 1933) is somewhat less than that of *S. oleraceus*. Achenes of *S. asper* have been collected by aircraft on a screen 2000 ft. above Tallula La. (Glick, 1939).

(*d*) *Viability of seeds; germination.* Achenes were found to have retained 27 % viability after passing through the digestive system of a cow (Dorph-Peterson, 1924). Viability of two samples collected from soil was 92 and 81 % respectively, and viable achenes were found in arable land at depths down to 25 cm. (Buchli, 1936).

(*e*) *Seedling morphology.* Fig. 4.

X. *History.* Dunn (1905) suggests that *S. asper* may be a native of bare sandy hills around the Mediterranean Sea. Achenes have been recorded from the Elephant bed overlying London clay at Clacton-on-Sea—a 'warm climate' interglacial deposit (Warren, 1923), and (probably this species) from upper fine-detritus mud in post-glacial lacustrine deposits from Co. Meath, Ireland (Zone VIII: Mitchell, 1940).
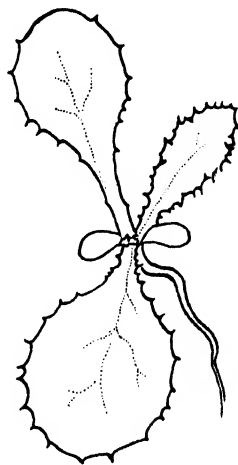
Fig. 4. Seedling of *S. asper*, 2 weeks old (× 2). (Note base of lamina gradually tapering into petiole.)

General. *Economic importance.* The use of sowthistles as potherbs ranges from Europe to the Antipodes, and dates from ancient times. Pliny recounts that Hecale regaled Theseus with a dish of *Sonchus* sp. before he went out to slay the bull of Marathon, while Fitter (1945) records their use by the poor in fifteenth-century London. (Theophrastus derives the generic name from the Greek—σόος = sound, and ἔχειν = to keep—hence salubrious!) The plants feature in many herbal remedies, and, by the doctrine of signatures, the presence of latex is taken to indicate a specific influence on lactation in human beings and in animals. Gum cathartic, prepared from the latex of *S. oleraceus*, appears in the U.S. Dispensatory, where its use is suggested for treatment of the opium habit.

Sonchus spp. are said (Hegi, *Fl.* **6**, 2) to be sown occasionally in Switzerland as a crop on which edible snails are raised: the only other use for these plants has been suggested by Kassner (1885), who investigated the possible utilization of *S. oleraceus* as a source of 'rubber'.

As weeds, however, both species are of considerable agricultural importance. The abundance and ready dissemination of the fruits, together with their rapid, high percentage germination, render them particularly well adapted to arable conditions, while the large size of the plants, together with their high potash uptake (about 5 % of the dry weight: cf. Long (1910) and Kassner (1885)) may result in considerable impoverishment of badly infested soils. In addition, several species of aphids may spread from plants of *Sonchus* spp. to cultivated crops, especially to lettuces and to currant and gooseberry bushes, while these weeds may also act as carriers for the mangold-fly (*Pegomyia betae*) and the nematode *Tylenchus devastatrix* (Long, 1910). Davis (1913) proposed the eradi-

cation of all *Sonchus* plants in the vicinity of *Pinus sylvestris* plantations, since he records *Sonchus asper* in Wisconsin to be infected by a European pine rust (*Coleosporium sonchi-arvensis*).

Pammel (1913) states that in certain cases these weeds may be controlled by sheep grazing, or by the application of ferrous sulphate solution. It is certain that a large measure of success can be obtained by surface cultivation of arable fields in winter or early spring, when this is possible, together with the mowing of waste places before flowering commences (Muenscher, 1935). A further suggestion has been made (Quilis Pérez, 1931) that such parasitic insects as *Cystiphora* spp., which effectively sterilize the capitula which they infest, might possibly be effective in the control of *Sonchus* spp. as weeds. The plants are affected, but not immediately killed, by application of methoxone (Clements, 1946).

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* An asterisk indicates that the reference has been taken from Biologica Abstracts, etc., and the original paper has not been consulted.

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ERRATA

C. B. Williams. The logarithmic series and its application to biological problems.
J. Ecology, **34**, (2).

On p. 261, 3rd line below table, and on p. 272, no. IX, 3rd formula,

for $\dfrac{e^{S/\alpha} - 1}{e^{S/\alpha}}$ read $\dfrac{e^{S/\alpha} - 1}{S/\alpha}$;

also on p. 266, Table 6, 4th line,

for   14220; 15813; 17331 and 18772,

read   14083; 15607; 17124 and 18634.

The error also occurs in the original table in *J. Anim. Ecology*, **12**, 55.

THE WATER ECONOMY OF THE VEGETATION OF THE 'CAMPOS CERRADOS' IN SOUTHERN BRAZIL*

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(*With Plate* 20 *and* 31 *Figures in the Text*) ·

CONTENTS

1. INTRODUCTION

Very vast areas of southern and central Brazil are covered with a vegetation of savanna-like aspect, the 'Campos Cerrados'.† These were first described in a very thorough floristic monograph by Eugen Warming (1892), who spent nearly three years (1863–6) in Lagoa Santa, as an assistant of the famous Danish explorer, zoologist and palaeontologist, P. W. Lund. His description was published only in 1892; the classification of his rich new material had required a long time, and even then, it was incomplete.

The most outstanding features of the Campos Cerrados are the peculiar aspect, and the floristic composition of the vegetation. Small trees (5–8 m., Pl. 20, phots. 1 and 2), often with contorted and gnarled stems, are scattered over the land, permitting sunlight to reach the ground. This in the rainy season is covered by a great many lower (as a rule perennial) plants, part of which disappear from the surface in the dry 'winter' period, while the majority of the trees and shrubs may persist with their foliage until the next spring time. Shedding of leaves, when it occurs, is not quite regular; there are cases when all the trees and shrubs, or nearly all of them, are bare of leaves at the end of the dry period. In other years, or in the same years but in other habitats, most of them may retain their leaves the year around. Of special importance is the observation (Warming, 1892) that sprouting and unfolding of the leaves occur at the end of the dry season, independently of precipitation; often the trees and shrubs produce flowers and new leaves before the first rains.

The aspect of these 'Cerrados' recalls the orchard shrubs of the savanna formations in other regions, specially those of South Africa.

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† When the range lands are clean, they are called 'Campos limpos'. Where there are shrubs and some small trees, they are 'Campos sujos' (*sujo* = dirty), and where the shrub-like vegetation covers them more densely, they are 'Cerrados' (*cerrado* = dense). From the 'Campos Cerrados' to woodlands with a continuous forest-like cover there exist all degrees of transition. The floristic composition of the 'Campos Cerrados', however, is quite characteristic.

The existence of such extensive savanna-like vegetation is generally supposed to be due to the dryness of the climate. Botanists such as Schimper (1898a, b) and Wettstein (1904) emphasize this viewpoint, and climatologists (Trewartha, 1937) and pedologists (Setzer, 1946) share it. There are, however, contrary opinions. Thus Lund (cited by Warming, 1892) was convinced that the Cerrados of Lagoa Santa did not represent the natural vegetation, or as we should call it to-day, the climax. In his opinion, under undisturbed conditions, we should have here forests of a certain dry forest type, and the existence of the Cerrados is attributed by him to human interference, especially by fire. It is true that annually the regions of the Cerrados are burned intentionally in order to clean the fields and to promote a better and earlier sprouting of the grasses and herbs. This is a very common phenomenon in all tropical grasslands and savannas. There are other authors, too, who share Lund's ideas. A survey of these controversies is given by Frenguelli (1940) and Ferri (1943), and also by the writer (Rawitscher, 1942-4).

Probably there is truth in both views, since such a specialized vegetation type with so many adaptations to particular climatic and edaphic conditions, as we shall see later, must have been developed in a region where it constitutes the natural or climax-vegetation. These conditions certainly exist in some parts of South America, especially in central Brazil, where the rainless period is pronouncedly hot and dry. But probably the opponents are right too, because human interference, by felling the trees and burning the fields, created conditions which favoured the extension of the Cerrado vegetation far beyond its natural boundaries.

This problem, however, cannot be solved by theoretical discussions nor by incidental observation. Only a detailed examination of the water relations of the soils and of the vegetation can elucidate the ecological status of the Campos Cerrados. We need not insist upon the practical importance of such researches, for the possibilities of agriculture and silviculture, and the feasibility of irrigation measures, all depend on the water available.

2. ECOLOGICAL CONDITIONS

Figs. 1 and 2 give the position of the regions concerned. The Campos Cerrados are encountered in the Central States of Brazil, especially in Goyaz, Bahia, Matto Grosso, Minas Geraes and São Paulo. In the latter they reach their southern borderline at least in their typical development, although many components of this vegetation are found in the State of Paraná and farther to the south.

The climate of central Brazil is thoroughly tropical, especially in the lowlands and coastal plains. The highlands of the interior have a mountainous tropical climate of more temperate character. From São Paulo southwards there is transition to subtropical and temperate conditions. Thus, in a general way, we may distinguish with Martius (1840-1906) the following phytogeographical regions: *Nayas*, or the equatorial rain forest of the Amazon; *Dryas*, or the region of the rain forests (tropical in character) of the coastal mountains; *Napaea*, or the subtropical-temperate region of the south, characterized by the occurrence of *Araucaria brasiliana*; *Oreas*, the mountainous drier interior; and *Hamadryas*, or the driest regions of Brazil's north-east, characterized by the deciduous Caatinga forests (Fig. 3).

The studies here described were made in Emas (3 in Fig. 2); Lagoa Santa, studied by Warming, lies more to the north (4 in Fig. 2), but conditions and vegetation there are

rather similar. Table 1 and Fig. 4 give the mean temperatures and precipitations from Ribeirão Preto, near Emas. As average values, however, are not sufficient for ecological purposes, we add a graph showing the march of temperature (maxima and minima), and the daily precipitation in Emas, for a typical year (1943). We see that the temperature maxima in winter are not much inferior to those of the summer; the minima, however, are much lower and sometimes freezing-point is reached. These low winter temperatures are characteristic of the south. At Belo Horizonte or Lagoa Santa temperatures below 0° C. are not recorded.

Rainfall in the winter or dry season in these parts is very infrequent, but when it occurs it may be heavy. The driest months are May–August, generally with fair, cloudless weather. Evaporation in this period is great, and relative humidity in the noon-time hours can be

Fig. 1. Map of Brazil.

very low (20%). Under such conditions a month with less than 60 mm. precipitation is regarded as arid. It is true, however, that the daily evaporation is lowered by the short duration of the day. The thirteen dark hours (Fig. 6), with heavy radiation lower the temperature during the night and bring the relative humidity values to 100%. Thus, at sunrise, the fields, at least in May, June and July, are generally covered with dense mist. Thus evaporation is insignificant or absent (Fig. 7) during a great part of the night (dew begins to fall as early as 8 p.m.), and it begins only after the fog has been dissipated, at 9 or 10 a.m. Near the end of the dry period, however, the air is drier, relative humidity reaches low values, and fogs are rare; the mornings begin with positive evaporation values. These latter depend both on relative humidity and air movement. Measurements with the Piche evaporimeter give higher values when winds (frequently short heavy spells) blow (Fig. 8).

Publications concerning the soil of our region are scarce. The soil maps that exist are, ecologically at least, of little use (see Camargo & Vageler (1940), p. 5), and as we showed elsewhere, soil differences depend much on the degree of deterioration and leaching produced by its historical development, as well as its inherent qualities (see also Rawitscher, 1942–4, 1946). In addition to this, soil investigations often restrict examination to the top 1·5 m. In this instance, however, the deeper layers are of great importance.

Fig. 2. Map of southern Brazil. (1) Iguassú falls; (2) the mouth of the Tieté river; (3) position of Emas (Pirassununga); (4) Lagoa Santa.

The most important fact for our studies is the great depth of rock decomposition in all the humid tropical regions. Here the bed-rock often cannot be found at less depth than 20 m. Above the soil is a homogeneous reddish loamy earth without stones or pebbles. We have no detailed analyses, and limit ourselves to the statement that the soil in the fields is certainly not infertile (as already stated in a general way for the region, by Löfgren, 1890, p. 12), because the same land, nearby, when cultivated, without fertilizers, yields good crops of fruit (Pl. 20, phot. 2) or sugar cane. The pH was near 5·0.
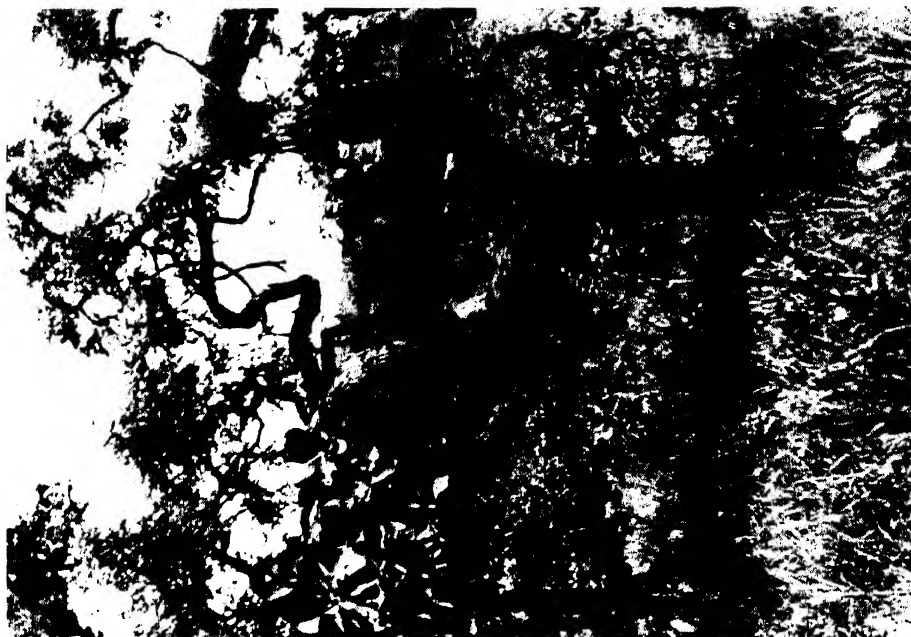
Phot. 2. Campo Cerrado at Lagoa Santa with *Dalbergia violacea* and *Kielmeyera coriacea* (left).

Phot. 1. Aspect of Campo Cerrado (Emas) with *Kielmeyera coriacea* (foreground) and *Dimorphandra mollis*. The grass is mainly *Echinolaena inflexa*.

Since it was necessary to know the water-content in the different layers we opened three wells reaching the ground water-table at 17–18 m. As the wells were drilled at the highest levels of the rolling land, ground-water here could not be conducted from elsewhere and must have been derived from the excess of the summer rains *in situ*. The ground-water table is continuous, and the many wells that exist in the region for household purposes indicate, in comparable cases, similar depths of the same continuous ground-water. Fig. 9 shows the distribution of water, air and solid matter determined in such an excavation.
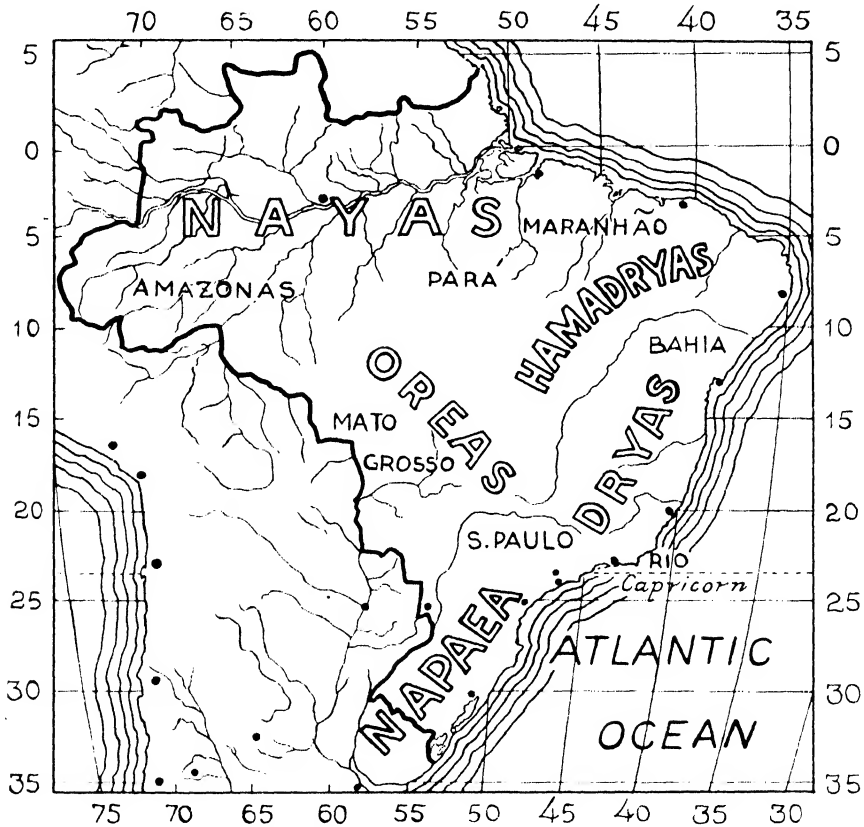
Fig. 3. Main phytogeographical regions of Brazil; after Martius.

From this ground-water there drains off throughout the year, even at the end of the driest periods, water that feeds springs and streams.* In the State of São Paulo these seem never to fail, but in the drier north of the State of Minas Geraes there are regions, where in the dry season streams and rivers are dry. This significantly is the case only under forest cover, and ceases when the forests are felled and replaced by less heavily transpiring field or shrub vegetation (Silveira, 1923).

In the Campos Cerrados of Emas there is no superficial erosion, and this is so over the greater part of our region except where the ground has been artificially cleared of vegetation. Even during the heaviest rains, no puddles form and no water flows over the surface

* The well of the railway station adjacent to our fields and situated at the top of the ridge yielded 1 cubic metre of water daily without diminution even at the end of the dry period of the excessively dry year 1944.

Table 1. *Temperatures, 1901–17*

Ribeirão Preto, lat. 21° 10′ 7″ S.; long. 47° 48′ 4″ W.; alt. 556 m.

Month	Mean (° C.)	Mean (max.) ° C.	Mean (min.) ° C.
Jan.	23·4	29·9	18·3
Feb.	23·9	30·9	18·7
Mar.	23·3	30·3	17·7
Apr.	21·6	29·3	15·1
May	18·5	27·0	11·4
June	17·4	25·9	10·5
July	17·4	26·9	9·4
Aug.	17·0	31·0	10·8
Sept.	21·4	30·3	14·1
Oct.	22·5	30·3	15·7
Nov.	23·4	30·7	17·3
Dec.	23·5	30·1	18·1
Annual average	21·2	29·5	14·8
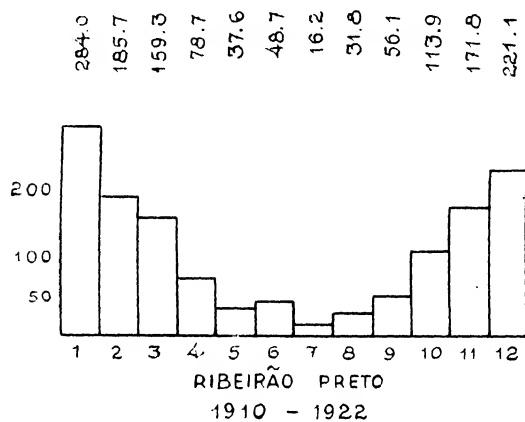
Fig. 4. Monthly precipitation values (mm.) in Ribeirão Preto.
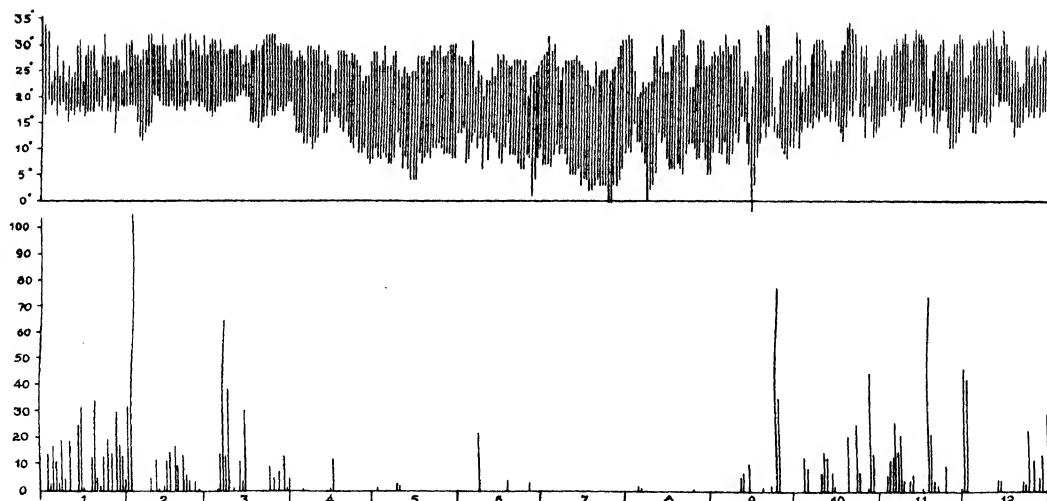
Fig. 5. Daily range of temperature (above), and precipitation (mm.) (below), during the year of 1943.

of the soil. Only where the soils are sunbaked and hard do we find sheet erosion or forma-
tion of gullies, as in overstocked range, clean fallow land, and coffee plantations free from
ground cover.
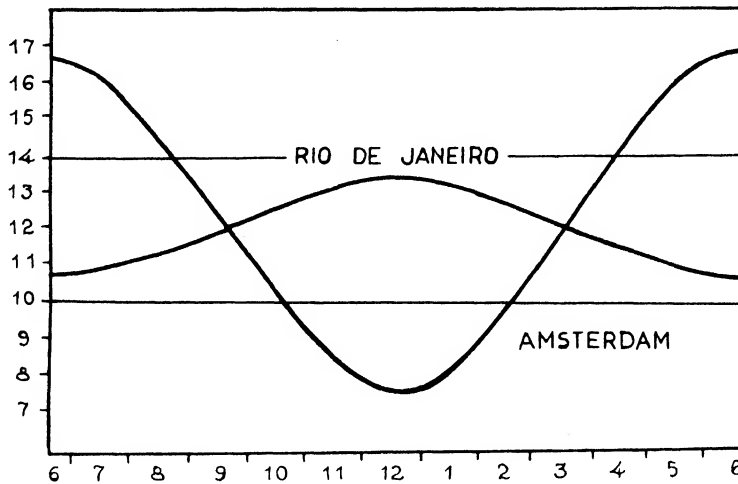
Fig. 6. Length of the day, in hours, during the year, in Amsterdam and Rio de Janeiro.
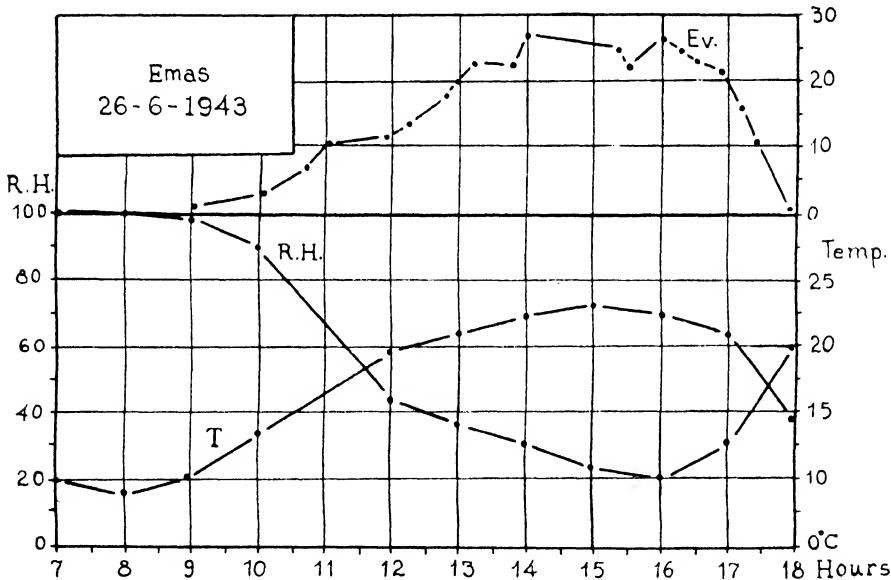
Fig. 7. Evaporation (Piche evaporimeter), relative humidity and temperature, during a typical day at the
beginning of the dry period, in Emas.

The actual density of population is not very great, but there is no part of the Campos
that is not used, at least for extraction of firewood and tanbark, or for grazing. Fires are
intentionally started every year in the middle or end of the dry period in order to promote
an earlier and better sprouting of the grasses. Colonization by White Man took place
about 1820 (Godoy, 1946), but we are sure that the Whites did not discover the region in

a perfectly natural condition. Population of the Amerinds (Tupy-Guarany) was relatively dense in these times and artifacts, especially pottery, are frequently found in the region (Fig. 10). It is true that Emas was a place of concentration because of the excellent fishing conditions in the cataracts of the River Mogy-Guassú, but as Godoy points out, the aborigines lived largely on the vegetable products which were exploited not only for food but for many other purposes, yielding material for construction and thatch (Indaya-palm, Attalea Loefgrenii), fibres for nets and other textiles, and especially, firewood. Indians are 'inveterate burners' as Myers (1936) puts it: 'The scattered aboriginal Indians are inveterate burners. It is almost impossible to prevent one's Indian carriers from setting
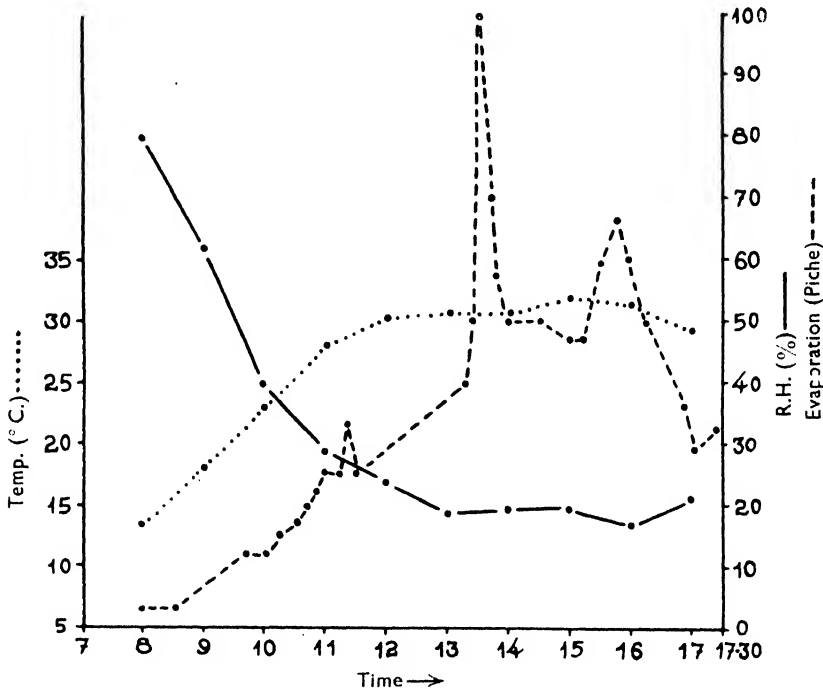
Fig. 8. Evaporation (Piche evaporimeter), relative humidity and temperature, during a typical day at the end of the dry period, in Emas (27 August 1943); after Ferri.

light to the dry grass. They do this to signal their approach and for pure fun. I have never seen in South America a savannah however small or isolated or distant from settlement which did not show signs of more or less frequent burning. The ranchers burn to destroy the roughage and encourage young tender growth for their stock.... The main savannah plants, notably *Trachypogon plumosus*, *Paepalanthus capillaceus* and *Curatella americana*, are so eminently adapted to burning, which they almost invariably survive, that we are justified in regarding the present vegetation as a fire climax (subclimax in Clements' terminology).'

Such burning, over long periods, may have altered the vegetation so much that the true climax is not only unrecognizable to-day, but may have ceased to exist already before the first periods of colonization. Many researchers suppose the same thing for the vegetation of all the continents (Rawitscher, 1942–4).

The vegetation is made up by small trees, tree-like shrubs, small shrubs, herbs, climbing plants and a very few epiphytes; but it is difficult to classify the components of the community thus. Nearly all the plants are perennial, and a good many of the species appear, depending on the conditions, sometimes as herbs or shrubs, sometimes even as
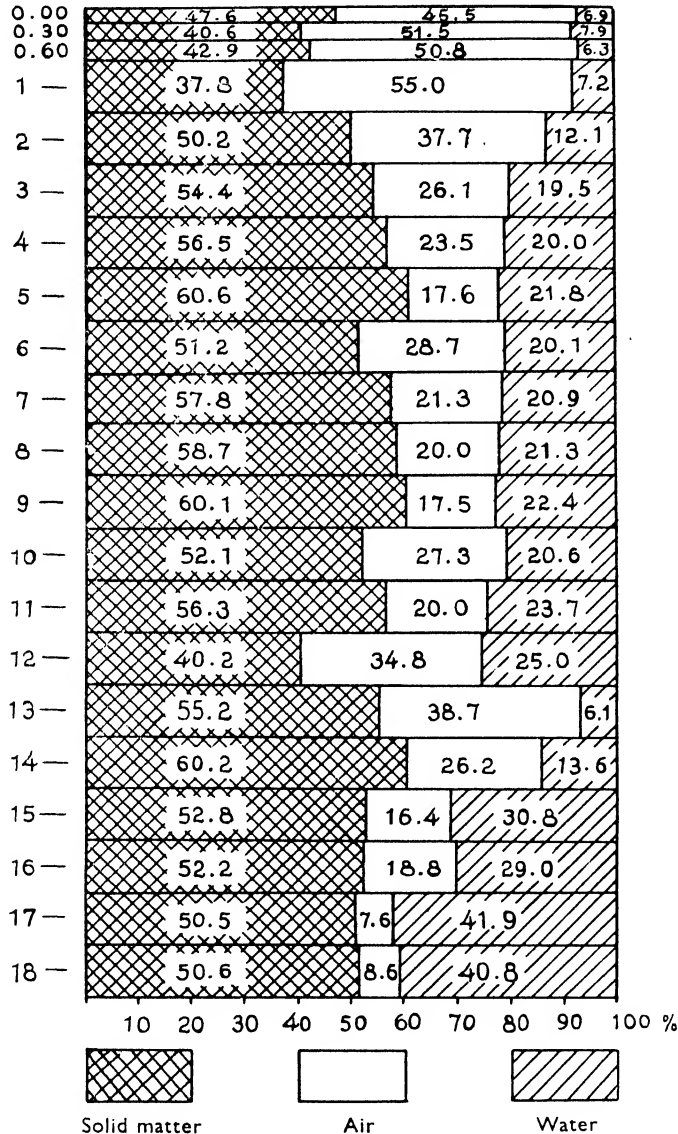
Fig. 9. Soil profile down to the water-table at 18 m., in volume-percentage.

trees. For instance, *Lippia lupulina*, as I. Schauer, the author of the *Verbenaceae in Martius' Flora*, points out, is herb-like when collected in Campos that recently have been burnt, but where for a longer time fire has been excluded, it is a shrub. *Caryocar brasiliensis* in many regions is a beautiful shade tree, as, for example, in the protected graveyard that contains Lund's tombstone at Lagoa Santa (Ferri, 1943). In Emas, where fire

is a regular annual phenomenon, *Caryocar* does not differ much from a herb, or a very low shrub, with most of the ligneous, permanent parts, in the soil.

There are other types that above-ground *always* appear like herbs, having lost the power of forming permanent stems or twigs above the surface. Some of these, like *Andira humilis, Anacardium pumilum, Jacaranda decurrens*, and certain *Anona* species, pertain to genera of which the other species are trees or higher shrubs. They have been spoken of as 'subterranean trees', in reference to the often enormous development of their subterranean, ligneous parts (see Fig. 11).
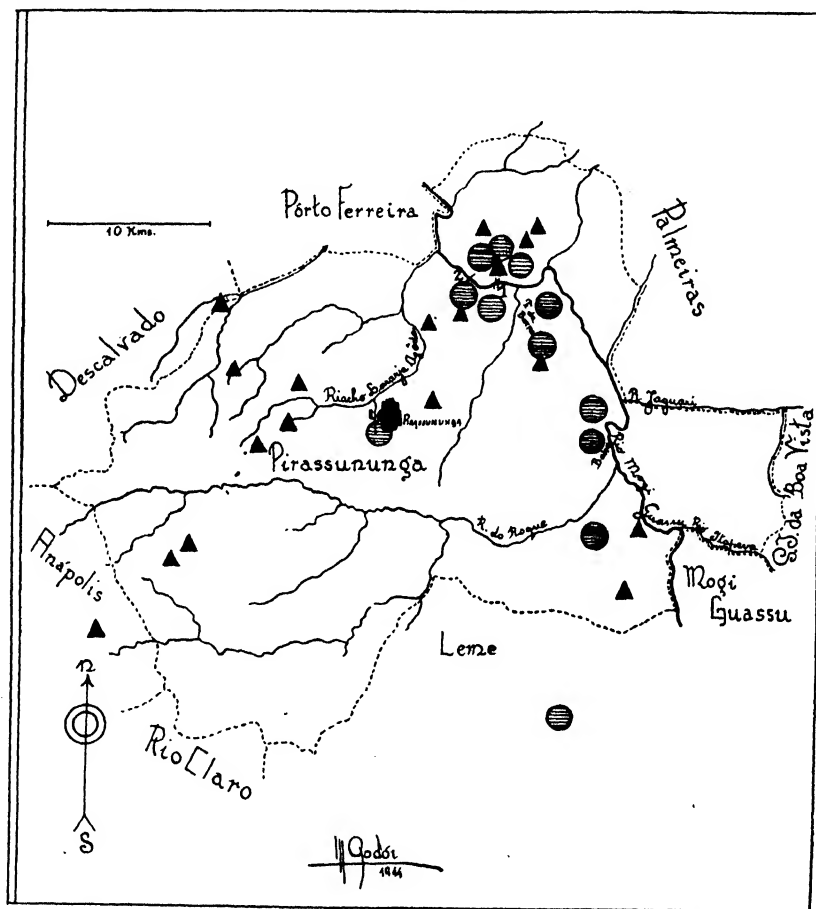
Fig. 10. Relics of Pre-Columbian Man in the region of Emas (Pirassununga); after Godoy.
⊕ Pottery.   ▲ Stone instruments.   (1) Falls of Emas.   (2) Cataracts.

Just as there exist many transitions between trees, shrubs and 'herbs', so it is difficult also to distinguish between plants that regularly shed their leaves in the dry season, and others that retain them. Periodicity here seems to be less inherent than that of the tropophytes in temperate climates, at least for most of the plants (exceptions: certain Bombacaceae, Leguminosae and others). Shedding of leaves varies with the local conditions.

The best basis for distinguishing ecological groups seems to be the nature of the root systems. If these go deep enough to reach the permanently wet lower soils, plant transpiration will be relatively unrestricted. These plants can retain their foliage through the

dry season and they *can* develop, when other conditions such as fire, cutting, grazing, and so on, allow this, into trees, or shrubs, often preserving their leaves all through the rainless period. On the other hand, there are plants with shallow root-systems which *cannot* show a greater development above ground, even if protected against human and animal interference. They must shed their leaves in the dry periods, and often only their subterranean parts survive. But we are far from knowing the root-depths and the subterranean morphology of all the plants composing our vegetation; thus we can only present here a preliminary list of the plants of Emas, which are found to belong to the phanerophytic and often nearly evergreen part of the vegetation, generally with deep roots; and on the other hand, of the cryptophytic plants that in the dry period disappear completely or nearly completely from the surface. A third group is constituted by grasses, which vegetate abundantly in the rainy period and survive in the first part of the dry period; later on, they
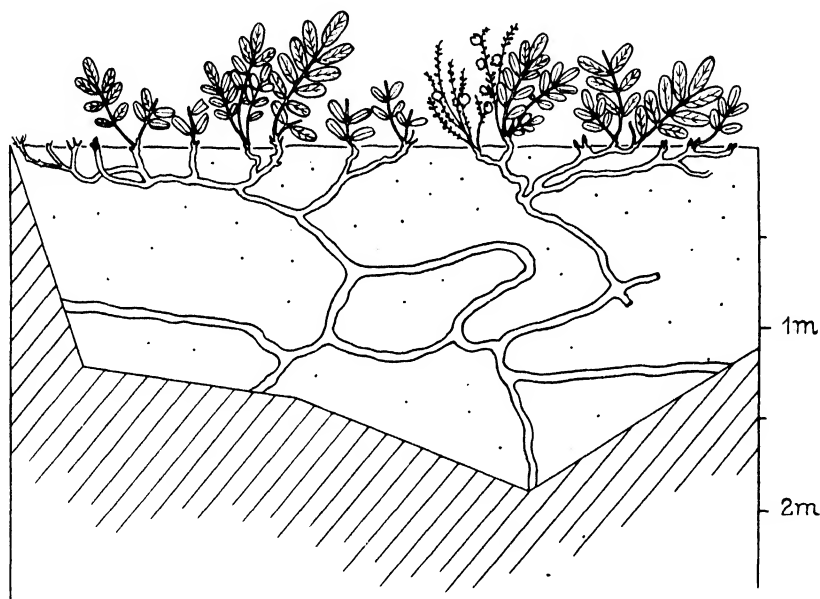
Fig. 11. Section through the upper part of the soil with *Andira humilis*. Down to 2 m. there are formed, generally, only storing roots. Absorbing roots were encountered down to 18 m., where the water-table was reached.

dry up, and it is the bulk of their brown dry leaves that specially feeds the fires. At Emas, drying of the grass as a rule occurs when the water content of the soil near the rhizosphere falls to between 8 and 6 % dry wt.

List of characteristic Cerrado plants at Emas

(1) *Deep-rooted*

(*a*) Evergreen or nearly so at Emas

Dimorphandra mollis Benth. (Legumin.)
Stryphnodendron Barbatimão Mart. (Legumin.)
Andira humilis Mart. (Legumin.)
Sweetia dasycarpa Benth. (Legumin.)
S. elegans Benth. (Legumin.)
Machaerium acutifolium Vog. (Legumin.)
Dalbergia sp. (Legumin.)

Copaifera Langsdorffii Desf. (Legumin.)
Connarus suberosus Planch. (Connarac.)
Kielmeyera coriacea Mart. (Ternstroemiac.)
Tocoyena formosa Schum. (Rubiac.)
T. brasiliensis Mart. (Rubiac.)
Palicourea rigida H.B.K. (Rubiac.)
Strychnos Pseudo-Quina St Hil. (Loganiac.)
Anacardium pumilum St Hil. (Anacardiac.)
Byrsonima coccolobifolia Kth. (Malpighiac.)
B. verbascifolia Rich. (Malpighiac.)
Erythroxylum suberosum St Hil. (Erythroxylac.)
E. tortuosum Mart. (Erythroxylac.)
Caryocar brasiliense Cambess. (Caryocarac.)
Didymopanax vinosum E. March. (Araliac.)
Aegiphila Lhotzkyana Cham. (Verbenac.)
Qualea grandiflora Mart. (Vochysiac.)
Ouratea spectabilis (Mart.) Engl. (Ochnac.)
Anona coriacea Mart. (Anonac.)
A. dioica St Hil. (Anonac.)
Duguetia furfuracea (St Hil.) Benth. & Hook, Fil. (Anonac.)
Neea theifera Oerstedt (Nyctaginac.)
Piptocarpha rotunda (Less.) Baker (Compositae)

(b) Summer-green trees, depth of roots probably great, but not yet determined

Tecoma Caraiba Mart. (Bignoniac.)
Aspidosperma tomentosum Mart. (Apocynac.)
Bombax gracilipes Schum. (Bombacac.)

(2) *Shallow rooted, summer-green*

Craniolaria integrifolia Cham. (Martyniac.)
Collaea decumbens Benth. (Legumin.)
Centrosema bracteosum Benth. (Legumin.)
Cassia cathartica Mart. (Legumin.)
Vitis salutaris Baker (Vitaceae)
Waltheria communis St Hil. (Sterculiac.)
Helicteris brevispira St Hil. (Sterculiac.)
Rhodocalyx rotundifolius Muell. Arg. (Apocynac.)
Macrosiphonia verticillata Muell. Arg. (Apocynac.)
Dipladenia gentianoides Müell. Arg. (Apocynac.)
Ipomoea villosa Meissn. (Convolvulac.)
I. procurrens Meissn. (Convolvulac.)
Lippia lupulina Cham. (Verbenac.)
Salvia rosmarinoides St Hil. (Labiatae)
Eriope crassipes Benth. (Labiatae)
Hyptis eriophylla Pohl (Labiatae)
Ruellia dissitifolia (N. ab. Es.) Hiern. (Acanthaceae)
R. geminiflora (N. ab. Es.) H.B.K. (Acanthac.)
Poikilacanthus humilis Lindau (Acanthac.)
Perianthopus Espelina Manso (Cucurbitac.)
Vernonia grandiflora Less. (Compositae)
V. bardanoides Less. (Compositae)
Isostigma peucedanifolium Less. (Compositae)
Aspilia reflexa Baker (Compositae)
Calea platylepis Schultz Bip. (Compositae)

(3) *Intermediary between deep and shallow rooted*

Butia (Cocos) *leiospatha* (Barb. Rodr.) Becc. (Palmae)
Diplothemium campestre Mart. (Palmae)
Acanthococos sp. (Palmae)
Jacaranda decurrens Cham. (Bignoniac.)
Cochlospermum insigne St Hil. (Cochlospermac.)
Manihot tripartita Muell. Arg. (Euphorbiac.)
Serjania erecta Radlk. (Sapindac.)
Solanum grandiflorum Ruiz & Pavon (Solanac.)

(4) *Grasses*

> *Echinolaena inflexa* (Poir) Chase.
> *Tristachya leiostachya* Nees.
> *T. chrysotrix* Nees.
> *Eragrostis perennis* Doll.
> *Axonopus longecilius* (Hack) Parodi
> *Andropogon paniculatus* Kunth.
> *Paspalum erianthum* Nees.
> *P. carinatum* Fl.
> *Aristida circinalis* Lindm.
> *A. megapotamica* Sprengel
> *Sorghastrum minarum* (Nees.) Hitchc.
> *Trachypogon canescens* Nees.
> *Panicum olyroides* H.B.K.

3. METHODS

On account of their great depth the soils could not be studied merely by digging trenches and pits; wells had to be opened by professional well-diggers. Soil samples were collected in at least every metre, and the roots encountered were sorted out for each depth level. The connexion of the deeper roots with the plant above ground could not be preserved, and identification, which therefore depends on anatomical particularities of the roots, is very difficult. In the upper layers we followed the connexion of the storing and absorbing parts of the root systems by careful excavation with special trowels. Water content of the soil was determined in percentages of dry weight and volume.

Now it is true that percentage of water does not give information on water available to the plants, which is generally determined by special methods. These, however, are not entirely satisfactory for deep soils, where the behaviour of each sample *in situ* may be quite different from what it would be after transport to the laboratory. For ecological purposes the study of the transpiration rate is a better index. If the plants transpire freely, without wilting or showing water deficit of the leaves, we are certain that they draw water from the ground, and if we know the depth of the roots, we know that the soil-layer contains available water. If, on the other hand, we see that particular plants wilt definitely when the soil-layer around their roots reaches a certain percentage, let us say about 6 % of water, as is the case when definite wilting in Echinolaena grass occurs in our fields, then we can say that here we reach the limit of water availability to these plants. (In layers deeper than 30 cm. the soils loose almost no water by direct evaporation, as was shown by Rotmistroff (1926), and water loss is indirect, by root absorption only.) Therefore, after the occurrence of permanent wilting, this percentage is nearly stationary until additional water is available.

Thus, from the root depth and the transpiration behaviour of certain plants, we can tell whether there is water available in particular layers of the soil. The plant ecologist will, therefore, use the refined methods of transpiration research which have been developed in the last two decades. These methods have been used already in such a great number of ecological studies (Stocker, 1929–35; Harder, Filzer & Lorenz, 1933; Huber, 1927; Stålfelt, 1932; Heilig, 1931; Bosian, 1933; Pfleiderer, 1933; Pisek & Berger, 1938; and Pisek & Cartellieri, 1931, 1932, 1939) that we need not explain them here in detail.

The course of the transpiration of the Campo Cerrados plants was followed especially by the methods of rapid weighing and infiltration. Infiltration by such liquids as petrol ether, xylol, alcohol and liquid paraffin, gives an easy first orientation.

Successive weighing of several leaves was done at intervals of 1 or 2 min. During the first minutes after being severed the leaf stomata are unaffected. Soon, however, when the water content in the leaf decreases, the stomata in leaves with a sensitive stomatal mechanism may begin to close. Thus we obtain not only the values of the initial transpiration, but also indications of the rapidity of closure, and finally, when closure is achieved, the cuticular transpiration.

We may illustrate this by means of Table 2, and Fig. 12, after M. Rachid (1947).

Table 2

$T = 29.7°$ C.; R.H. $= 52\%$; 1 December 1944

No. 1 *Aegiphila Lhotzkyana* Cham. Surface* of the leaf $= 94.6$ cm.^{2}				No. 2 *Craniolaria integrifolia* Cham. Surface* of the leaf $= 98.8$ cm.^{2}			
Time	Weight of the leaf (mg.)	Loss of water (mg./min.)	Control infiltration	Time	Weight of the leaf (mg.)	Loss of water (mg./min.)	Control infiltration
15.28	1353		$=\begin{cases} x: \dfrac{\text{ep. sup.} \quad 0}{\text{ep. inf.} + + +} \\ e: \dfrac{\text{ep. sup.} \quad + +}{\text{ep. inf.} + + +} \end{cases}$	15.31.5	1496		$=\begin{cases} x: \dfrac{\text{ep. sup.} + +}{\text{ep. inf.} + + +} \\ e: \dfrac{\text{ep. sup.} + +}{\text{ep. inf.} + + +} \end{cases}$
		12.5				14	
30	1328			32.5	1482		
		12.5				14	
32	1303			33.5	1468		
		12.5				11	
34	1278			36.5	1435		
		12.5				8	
36	1253			37.5	1427		
		12.4				8	
41	1191			38.5	1419		
		10				7	
43	1171			40.5	1405		
		8				5.6	
45	1155			43.5	1388		
		7.5				2.3	
47	1140			46.5	1381		
		4.8				2.5	
57	1092			48.5	1376		
		3.7	$=\begin{cases} x: \dfrac{\text{ep. sup. } 0}{\text{ep. inf. } +} \\ e: \dfrac{\text{ep. sup.} \quad 0}{\text{ep. inf.} + +} \end{cases}$	58.5	1358	1.8	
16.07	1055			16.00.5	1356	1	$=\begin{cases} x: \dfrac{\text{ep. sup. } 0}{\text{ep. inf. } 0} \\ e: \dfrac{\text{ep. sup. } 0}{\text{ep. inf. } 0} \end{cases}$

* Surface means upper + inferior surface. $x =$ Infiltration by xylol. $e =$ Infiltration by petrol ether.

Two severed leaves, one of *Aegiphila*, the other of *Craniolaria*, were picked and placed immediately on two balances, side by side, in the shade of an open 'Rancho'.* The differences of weight give the transpiration losses of the two leaves that had nearly equal surface areas. These values diminish rapidly in *Craniolaria*, but in *Aegiphila* the decrease is much slower and less complete. Simultaneously with the measured leaves others were gathered from the same twigs and in similar conditions, in order to follow the stomatal behaviour by infiltration with xylol (x) and petrol ether (e).

The leaf of *Craniolaria* had lowered its transpiration in less than half an hour from 14 to 1 mg.; that of *Aegiphila* from 12.5 to 3.7 mg. At the beginning of the experiment

* The 'Rancho' was a kind of shack, constituted solely by a roof on poles.

both of the plants showed open stomata, i.e. in *Aegiphila* the upper epidermis was not entered by xylol. At the end of the experiment there was no infiltration at all in *Craniolaria*, but the inferior surface stomata of *Aegiphila* still gave access to xylol and petrol ether. Later on we shall see that *Craniolaria* belongs to the shallow-rooted plants that depend on the variable amount of soil water available in the rainy season. *Aegiphila*, on the contrary, has roots that reach the permanently humid deeper layers of the soil and, under favourable conditions, can vegetate through the dry season. Plants of this category, we shall see, often do not possess very efficient stomatal regulation.

In addition to the information concerning rapidity of stomatal closure we can also state the relation between cuticular transpiration to the total transpiration. If we suppose that at the·end of the experiment the *Craniolaria* leaf had its stomata perfectly closed (although this is not quite certain from the data presented), this relation of total to cuticular transpiration would be 14 to 1. In *Cedrela fissilis* we found (Rawitscher & Ferri, 1942) that it can reach 70 to 1.
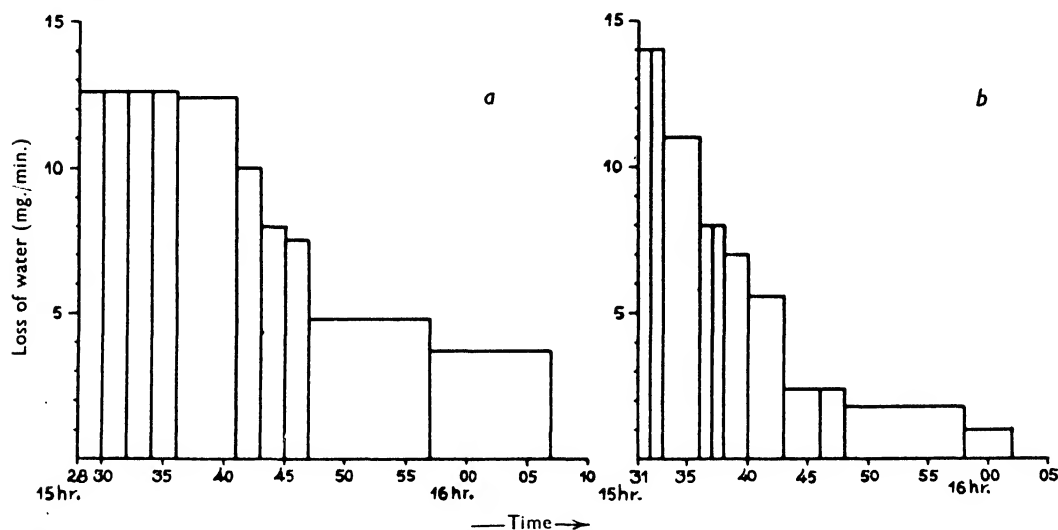
Fig. 12. Transpiration of severed leaves of *Aegiphila Lhotzkyana* (a) and *Craniolaria* (b), under identical conditions (1 December 1944; $T = 29.7°$ C.; R.H. $= 52\%$; *Aegiphila* surface $= 94.6$ cm.² and *Craniolaria* surface $= 98.8$ cm.²); after M. Rachid.

The initial values of total transpiration show a certain constancy in the first minutes. This can be expected, for closure will begin only when a certain deficit is reached, and with wide-open stomata the first contraction will not greatly diminish the rate of transpiration.

Table 3 records the results of another experiment described in the thesis of M. Rachid. One of the two leaves of *Aristolochia* had been in the shade, when collected, the other had been taken in sunlight. Infiltration with xylol gave maximum values in both of the control-leaves. The opening, however, must have been wider in the leaf from the sun, as we may conclude from the greater water loss. This accords with the later behaviour of the leaves. The leaf from sunlight gave signs of closing 10 min. after it was picked. When it reached the initial values of the leaf from the shade it had already lost over 300 mg. of water. The closing process is rather slow in *Aristolochia*; thus at 11.20, when the leaf was already rather dry, the stomata were not yet closed, and we may suppose that in such a state the closing mechanism will not work further.

In the leaves from the shade, on the contrary, closing is perceptible from the first, because when they were severed their stomata were less open, i.e. in a state where a slight closing produces a relatively great reduction. These stomata had time almost to complete closure. When the first signs of wilting were registered the leaf had lost 111 mg. of water and the rate of transpiration amounted to one-seventh of the initial, or to one-eleventh of the transpiration it would have shown if gathered in the sun. This leaf was able to close its stomata until not even petrol ether could enter. Table 3 represents one of several experiments with identical results.

Wide opening of the stomata constitutes a danger for plants exposed to rapidly changing water conditions. *Aristolochia Giberti* vegetates in the rainy season, when there is no

Table 3. Aristolochia Giberti *Hook.* (*stomata at the inferior side only*)

$T = 29 \cdot 2° – 30 \cdot 4°$ C.; R.H. $= 47–50 \%$; 8 December 1944

No. 1 (Leaf from the sun) Surface $= 187 \cdot 8$ cm.^{2}				No. 2 (Leaf from the shade) Surface $= 173 \cdot 4$ cm.^{2}			
Time	Weight of the leaf (mg.)	Loss of water (mg./min.)	Control infiltration	Time	Weight of the leaf (mg.)	Loss of water (mg./min.)	Control infiltration
10.47	2034		$= \begin{cases} x: +++ \\ e: +++ \end{cases}$	10.32	1533		$= \begin{cases} x: +++ \\ e: +++ \end{cases}$
		32				21	
48	2002			33	1512		
		32				19	
49	1970			34	1493		
		32				15	
52	1873			36	1463		
		32·6				8·5	
57	1710			38	1446		
		21·3				7	
11.16	1304		$= \begin{cases} x: \ ++ \\ e: +++ \end{cases}$	39	1439		
		19				6	
21*	1209			41	1427		
		17·5				5	
28	1086		$= \begin{cases} x: ++ \\ e: ++ \end{cases}$	42†	1422		$= \begin{cases} x: ++ \\ e: ++ \end{cases}$
						2·8	
				59	1374		
						2·3	
				11.02	1367		
						2·4	
				12	1343		$= \begin{cases} x: 0 \\ e: 0 \end{cases}$

* Leaf very wilted, folded and dry.   † Leaf wilting.

NOTE. Weight of the saturated leaf $= 1630$ mg.
Weight of the dry matter of the leaf $= 378$ mg.

severe drying of the superficial soil layers; it has rather deep roots, and maintains water reserves in its big 'xylopodium', as Lindman (1906) has called the subterranean intumescences so characteristic and frequent in the vegetation of the Campos Cerrados (Fig. 13).

Although the wide apertures do not constitute a danger for *Aristolochia Giberti*, they would be perilous for plants subject to brusque variations of water available to their leaves. This may be true in the case of real xerophytes, at least those of the non-succulent type, that maintain their roots in the superficial soil layers, but it may be valid equally for high trees, where not the water absorption, but water conduction may be the limiting factor. Although observations are as yet scarce, it seems that in such plants narrow
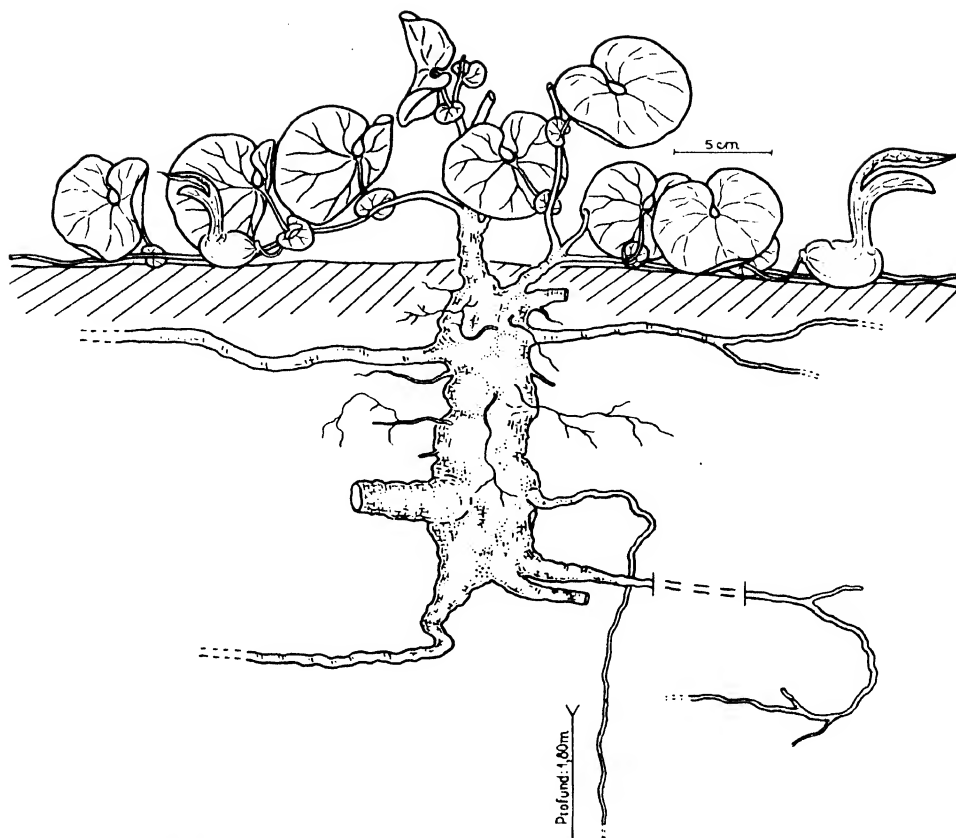
Fig. 13. *Aristolochia Giberti* (24 January 1944); after M. Rachid.
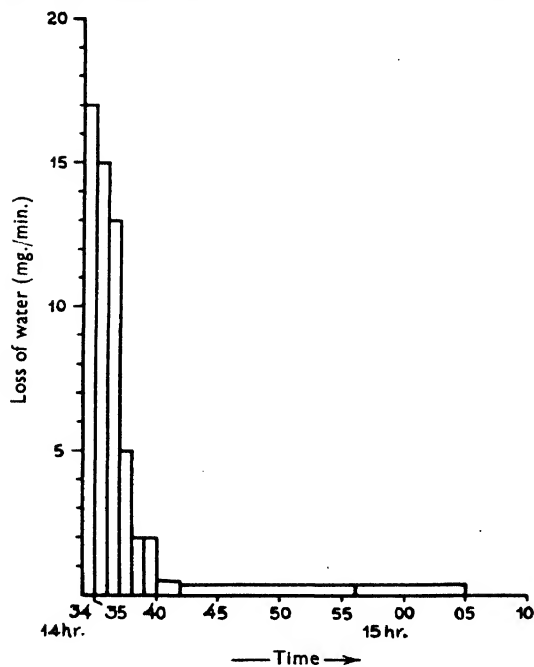
Fig. 14. Transpiration of a severed leaf of *Copaifera Langsdorffii* (21 September 1945; surface = 114 cm.²; $T = 31.7°$ C.; R.H. = 29%); after M. Rachid.

openings are frequent. This we found (Rawitscher & Ferri, 1942) in high forest trees, like *Cedrela fissilis*, where stomatal aperture never exceeds 2μ (Table 4), and in *Copaifera Langsdorffii* (Fig. 14). Table 4 and the graph show eloquently how very rapidly and efficiently the closing process can work in these cases.

Table 4. Cedrela fissilis, *leaflet*

$T = 20\cdot2°$ C.; R.H. $= 63\%$; 14 November 1941

Time		Weight (mg.)	Loss (mg./min.)
11.16	.	1553·5	
			7·5
17		1546	
			7
18		1539	
			7
19		1532	
			7
20		1525	
			6·5
22		1512	
			2
24		1508	

High and constant values of water loss at the beginning of a weighing experiment suggest, but do not prove, that we are dealing with nearly maximal stomatal apertures. (In nearly saturated leaves there may be found, due to other factors, such as illumination, inherent periodicity, etc., partially closed stomata with constant initial transpiration values, that decrease only when a greater water deficit is felt by the leaf.) In general, however, we may be certain that maximal transpiration is reached when the transpiration of a leaf attains 50–60% of the evaporation of a free-water surface. This is the case in the data of Stålfelt (1932), and similar values of transpiration/evaporation ratio were observed in other cases (sometimes over 70% in *Coffea* and *Cedrela* by the present writer, 1942).

Transpiration/evaporation ratio was determined by means of the 'Blatt evaporimeters' introduced by Kamp (1930) and Stålfelt (1932). A wet blotting paper, in size, shape and colour equal to the studied leaf, is placed on the balance and gives the value of the free evaporation in the same manner as we state the transpiration values of the leaf. In the case of the *Cedrela* leaflet (Table 4) the initial value of 7 mg. corresponds to 74% of the free evaporation. In this determination, cuticular transpiration was subtracted. To do that it was important to recognize that the cuticular transpiration is higher when a leaf is nearly saturated than when it is in a drier state, and when stomata are closed as a consequence of water deficit. For the cuticle also, to a certain degree, water is imbibed, and in a saturated leaf imbibition and in consequence cuticular transpiration will be higher.

What we wished to resolve in the first place was the question whether there is restriction or not in the transpiration of the plants during the day in the dry and in the humid season. To do this we followed the progress of transpiration of a great number of plants during the day, as was first done by Stocker (1931–5), for the vegetation of the Hungarian Steppe.

If there is no stomatal regulation, the transpiration values will follow the course of evaporation; if there is, the curves will differ characteristically. We need know only relative values of evaporation, measured with a Piche evaporimeter at the level of the transpiring leaves, and compare their daily curve with that of leaves picked at intervals from the same plant.

By simplifying and adapting the scheme given by Stocker (1931–5) we can characterize the essential types of transpiration behaviour in the following way (Fig. 15).

If *Ev.* represents the course of evaporation for a certain day, curve 1 indicates unrestricted transpiration with the stomata always equally open, and curve 3 may illustrate the cuticular transpiration when the stomata remain closed all day. In curve 2 the leaf stomata open in the morning, but later begin to close, partially or completely, losses approaching or reaching the values of cuticular transpiration. Stomata, then, may remain closed for the rest of the day, but very often we observe reopening, when the leaf has been able to overtake its water deficit. Of course there exist many transitions and alterations in the possible norms of behaviour of transpiration. Cuticular transpiration, too, may show a slight noon-time depression, and every case requires detailed study of all the conditions involved.
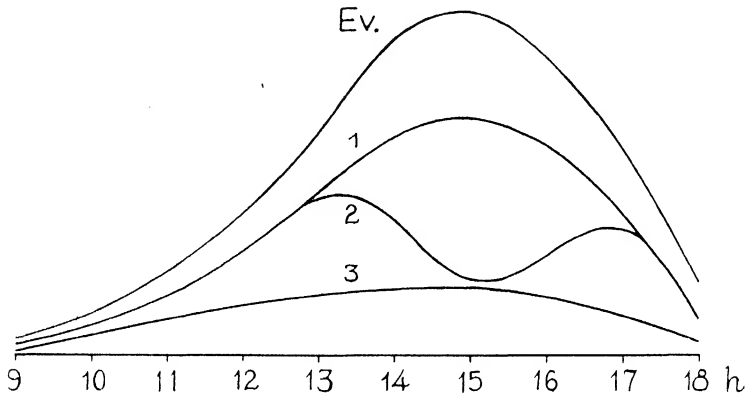
Fig. 15. Scheme of transpiration on a normal day. *Ev.* = evaporation; 1 = leaf which maintains the stomata open without regulation all day long; 2 = leaf partially closing the stomata during the driest hours; 3 = leaf with stomata closed throughout the day, showing only cuticular transpiration.

4. RESULTS

The most important results of our researches may be briefly summarized:

(a) Plants with deeply penetrating roots

Such plants explore the permanently humid layers of the soil, and generally show no, or relatively slight, restriction of transpiration in the dry period under the conditions of Emas. Here they are often able to maintain their foliage until the beginning of the rainy season, although certain plants, such as *Tecoma Caraiba*, *Aspidosperma tomentosum*, and *Bombax gracilipes*, shed their leaves regularly in the winter.*

The deepest roots were found in *Andira humilis* (Fig. 11). Considering that they penetrate the subterranean water-table even at 18 m., have very large ligneous vessels, and that the plant above ground is very small, it is not astonishing to find no restriction at all at the beginning and even at the end of the dry period, when drought is at its highest (Figs. 16 and 17). Nevertheless, *Andira* is capable of closing the stomata; this became evident when the roots of one of the specimens were laid bare, and partially injured: water conduction was damaged, the stomata began to close at noon, and the typical depression of transpiration, followed by a second short maximum, appeared (Fig. 18).

The behaviour of *Kielmeyera coriacea* was very similar. It is a relatively high tree (3–8 m.) with large leaves (Pl. 20, phot. 1), of rather mesophytic appearance. Its wide stomatal apertures, easily recognizable with vertical illumination under the microscope,

* A complete list is given by Warming (1892), p. 387.
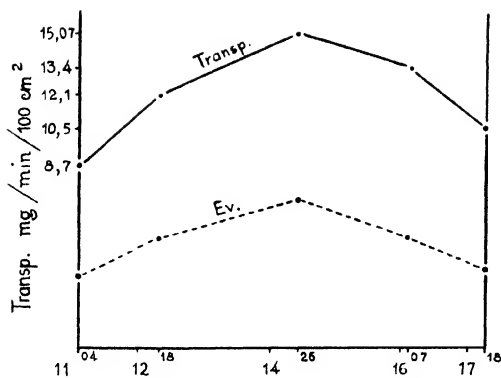
Fig. 16. Daily march of transpiration of *Andira humilis* at the beginning of the dry period (27 June 1943). *Ev.* = evaporation in relative values (Piche evaporimeter); after Ferri.
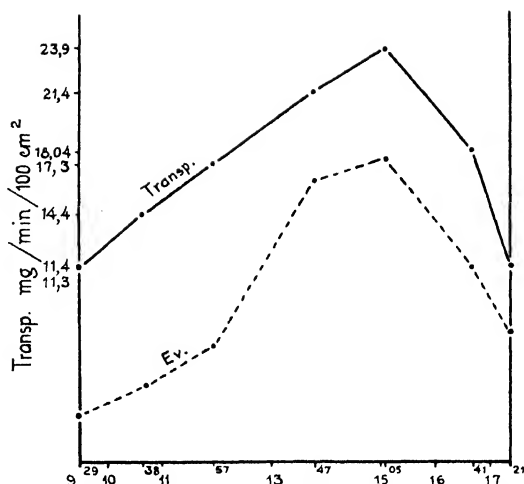
Fig. 17. The same as Fig. 16, at the end of the dry period (28 August 1943); after Ferri.
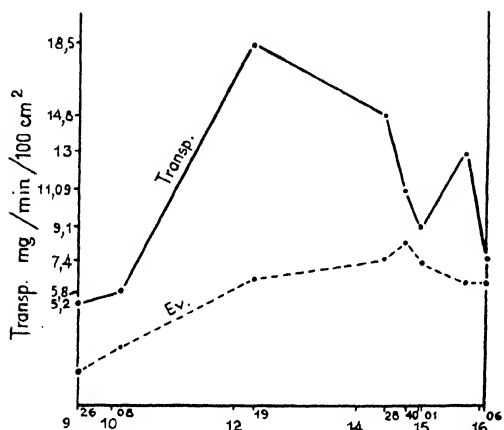
Fig. 18. Graph of transpiration of a plant of *Andira humilis*, the root system of which had been partially injured (24 June 1943); after Ferri.
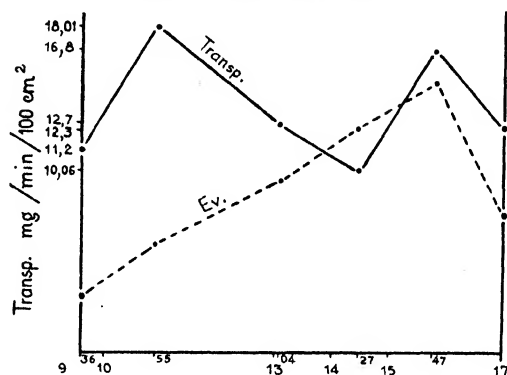
Fig. 19. Daily march of transpiration of *Byrsonima coccolobifolia* at the end of the dry period (27 August 1943); after Ferri.
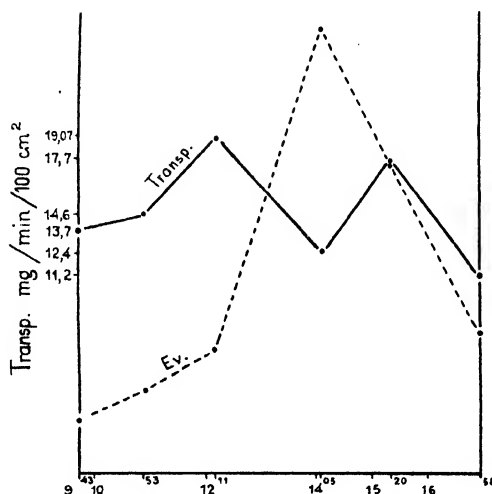
Fig. 20. Daily march of transpiration of *Anona coriacea*, at the end of the dry period (28 August 1943); after Ferri.

remained open the entire day, even at the end of the dry season. The graphs of transpiration did not differ much from those of *Andira*.

Others of the deep-rooted plants, however, showed a similar lack of restriction only in the first half of the dry season. In August the drought was heavy enough to produce slight noon-time, or rather, afternoon, depressions of the curves, as seen in *Byrsonima coccolobifolia* (Fig. 19) and *Anona coriacea* (Fig. 20). The latter plant showed slight depression already in the month of June.

In all these instances the diminution of transpiration did not lead to total closure of the stomata. Infiltration with xylol or petrol ether was nearly always possible in the great
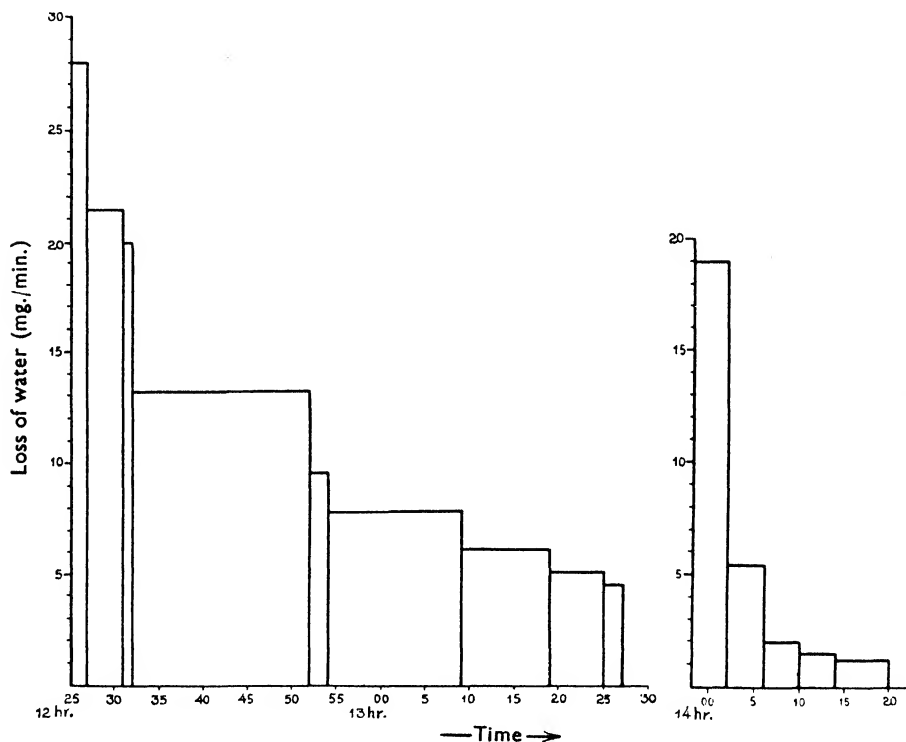
Fig. 21. Transpiration of a severed leaf of *Stryphnodendron Barbatimão* (left) and *Craniolaria* under comparable conditions (11 December 1943); after M. Rachid. Leaflet of *Barbatimão*: surface = 93·6 cm.²; T, from 24·2 to 25° C.; R.H. from 44 to 49%. Leaf of *Craniolaria integrifolia*: surface = 114 cm.²; $T = 25°$ C.; R.H. = 44%.

majority of the leaves. Indeed, when the leaves are severed from the plant, under dry noon-time conditions, they generally wilt in a few minutes without achieving stomatal closure. Fig. 21 shows the typical behaviour of such a leaf of a deep-rooted plant (*Stryphnodendron*, Fig. 22), in comparison with *Craniolaria* which belongs to the summer-green, shallow-rooted species.

The inertia of the stomatal mechanism is paralleled by a relatively inefficient cuticular protection, as was shown by Ferri (1944) for the majority of the leaves. Determinations, made by coating the lower side of hypostomatal leaves with vaseline, showed for *Andira humilis* and *Psychotria rigida* very high values (over 30% of the total transpiration) and only *Anona coriacea* gave as low values as about 2%.

In spite of the inefficient protection against water loss, the leaves develop such very small water deficits, expressed as percentage of the water of the saturated leaf, that even in the driest hours of the end of the dry season they could be considered as nearly saturated. (A greater deficit than 6% was not observed; these values are comparable only to the lowest indicated by Stocker (1931–5) for arctic vegetation of Lapland and grasses of the Baltic dunes.)

The deep-rooted plants, thus, under the conditions of Emas, generally do not suffer from lack of water; on the contrary, we may state that their leaves are adapted to a free use of it. The provisions of water stored in the soil and available to their roots are ample, and under the conditions of Emas they never fail.

On the other hand, consumption of water by the Campos Cerrados trees is relatively low; they have few leaves and conduction probably is not so serious a problem in these stunted plants as it would be in higher trees with a dense foliage.

For plants in such conditions a rapidly operating stomatal mechanism would be of little use, at least for adult specimens with deep roots. Should drought ever reach their rhizosphere, at the end of the winter, then definitive closing of the stomata would be necessary for all the rest of the dry period until the new summer rains should have reached the deeper layers. In this case shedding of the leaves is the better response. This is the reaction which seems to occur, as a rule, in the dry regions where the Campos Cerrados vegetation represents the

Fig. 22. Scheme of root systems of *Stryphnodendron Barbatimão* and of the *Echinolaena* grass, followed down to 2 m.

natural climax. At Emas shedding of leaves is found especially in young plants, the roots of which probably are not yet deep enough; their behaviour, and the rapidity with which their roots reach the permanently moist deep soil layers, has not yet however been studied methodically.

(b) Summer-green plants with shallow roots

While the potentially evergreen plants maintain the bulk of their absorbing roots in the permanently moist layers of the soil, the summer-green vegetation explores the more superficial layers that are periodically dry. Table 5 shows the penetrating of the drought from the end of the rainy season (March) to the end of the dry season. The surface (0·30 cm.) in the wet season, as in the dry, can desiccate by direct evaporation to a water content of 4–6%, which is near to the value for hygroscopic water (provisory determination by M. Rachid). When in the deeper layers the water content is as low as 6–8%, then the

wilting of grasses like *Echinolaena* is observed in the field. This occurs as a rule at the end of June or in July. Once the field is dry and brown, water content in the uppermost few metres is rather stationary, showing in different years oscillations due to the variability of the seasonal precipitation.

Table 5. *Water content in percentage of dry weight in the soil. Emas (Pirassununga)*

Depth (m.)	18. iii. 43	23. vi. 42	27. vii. 42	11. ix. 45
0·00	5·7	5·5	5·7	4·5
0·30	11·8	6·0	7·7	6·6
0·60	14·8	8·4	5·8	7·2
1·00	14·6	9·4	7·5	8·1
1·50	——	9·9	——	9·8
2·00	17·0	13·0	9·5	10·3
3·00	18·7	13·6	14·0	12·2
4·00	17·6	—	14·0	14·1
5·00	16·7	16·0	14·1	14·6

Such conditions would be appropriate for annual plants, and, in fact, maize, rice and beans can be cultivated here in the summer after clearing. The natural vegetation, however, is composed nearly exclusively of perennial plants, and the ground-cover in the rainy season is so dense that the seedlings have to struggle for place. Perennial plants which survive the drought below the surface have better chances. Digging in the soil we always find, besides the voluminous storing roots of the deep-rooted vegetation, the ample root-systems of the grasses and the many xylopodia of the summer-green plants. The water content of xylopodia, even during the dry period, is considerable. In *Aristolochia Giberti* (Fig. 13) M. Rachid found 55·3% water in September 1945, but the big xylopodia of *Craniolaria* (Fig. 23) were found to have a water content at the rainy season of about 90%, and at the end of the winter, approximately 78%. This permits sprouting, in the spring, before the first rains fall. (Other values: *Aspilia reflexa*: 1·12, 75·4%; 17·9, 60·0%. *Viguieria*: 1·12, 77·5%; 17·9, 59·0%.)

Craniolaria has its roots in the upper 30 cm. and vegetates only in the summer. Then it generally finds much humidity as a consequence of the frequent and heavy summer rains, and the water of the xylopodium constitutes a reserve for the rainless days or weeks that may always occur (see Fig. 5). Nevertheless, the stomatal mechanism is much more sensitive and efficient than that of the deep-rooted plants, as we saw earlier (Fig. 12). The same is true for nearly all the summer-green plants with shallow root-systems.

We reproduce from the paper of M. Rachid another figure (Fig. 24) representing a very shallow-rooted plant, *Vernonia grandiflora*, without xylopodium. *V. grandiflora* can flower and fruit in the first year, but generally, at Emas, it perennates, as in the example figured, where there are scars left from the dry period burning. Fig. 25 gives the closing of the stomata in a cut leaf. Stomatal operation in the shallow-rooted plants is not always so very efficient, and generally does not equal the perfect mechanism of the forest trees, like *Cedrela* or *Copaifera*. This is only to be expected for low-growing plants that vegetate in the humid season only. But analysis of a great many plants by M. Rachid showed that as a very general rule they possess a considerably better closing mechanism than the deep-rooted plants.

Cuticular protection, too, seems better. *Craniolaria*, for instance, in 30–40 min. lowered the total transpiration to the cuticular value, a reduction to about 5%, and similar values were obtained in *Serjania erecta*, but in other cases the percentage was higher, as in
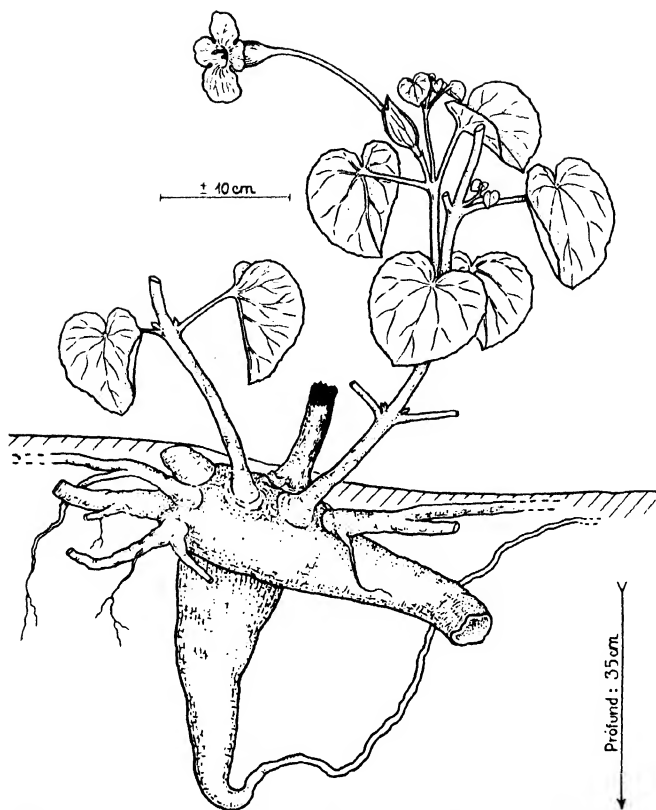
Fig. 23. *Craniolaria integrifolia* (10 December 1943); after M. Rachid.
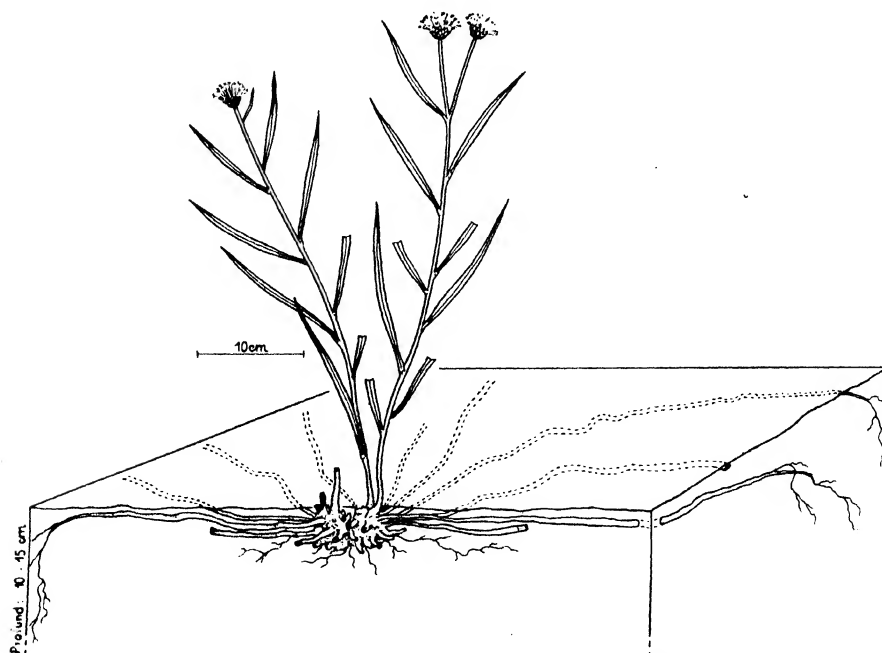
Fig. 24. *Vernonia grandiflora* (1 December 1944); after M. Rachid.

Cochlospermum, *Aristolochia* and *Manihot* (c. 10%), or *Poikilacanthus humilis* and *Collaea decumbens* (20%); in other species such as *Ipomoea villosa*, values of 30% were observed, but sometimes the stomata did not close completely, so that these values may include a fraction of stomatal transpiration.

Although the leaves, as a rule, are rather delicate and of a mesophytic type, where wilting would be easily recognizable, wilting was never observed in the fields during the rainy season. The water deficits seem always to be low, and sporadic determinations gave no higher values than 16·1%.

The summer-green vegetation, ecologically, seems to be less homogeneous than the deep-rooted part of the association. We already mentioned that the Campos Cerrados at Emas probably do not constitute the natural climax vegetation of this region. Clearing of the original forests may have opened the way for immigration of elements from the adjacent regions. The really deep-rooted plants seem nearly all to belong to the associations of the drier north, as we may conclude from the lists given by explorers, but the lower and
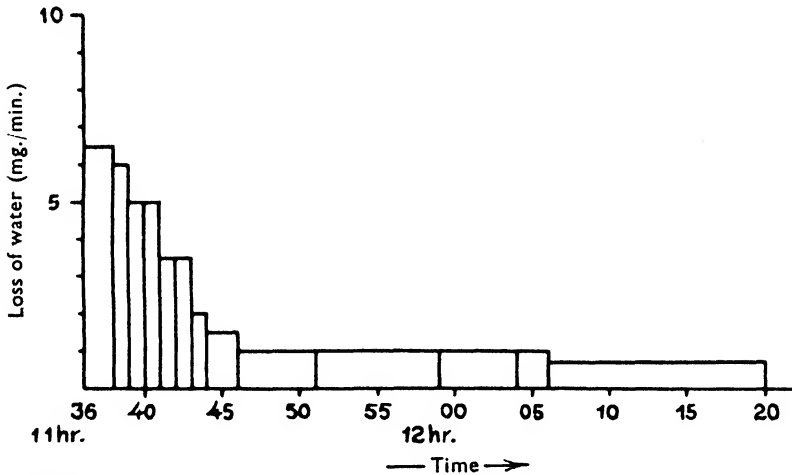
Fig. 25. Transpiration of a severed leaf of *Vernonia grandiflora* (8 December 1944); after M. Rachid. Surface = 19 cm.²; $T = 31°$ C.; R.H. from 45 to 49%.

less conspicuous plants often are unmentioned and it is not yet possible to group their associations. Thus further detailed investigations perhaps will show that the more drought-adapted shallow-rooted plants originally belong to the more xerophilous associations, whereas the less protected come from more humid regions.

One feature, however, they all must have in common, the capacity to survive the drought. Such subterranean organs as xylopodia are very frequent in the plants of the open Campos throughout Brazil, but in the Cerrado they display unusual dimensions. Fig. 26 shows the subterranean trunk of *Cochlospermum insigne*, a low shrub with conspicuous yellow flowers that appear in June in the dry season, when the plant is leafless. *Cochlospermum* seems to be a genuine inhabitant of the dryer north-east (Goyaz, Pernambuco). At the southern limit of the area (State of São Paulo) it seems to be progressing toward the south, occupying newly cleaned land along the roadsides and railways.

Often it is not easy to say if the xylopodia originate from roots or stems; in *Craniolaria* they seem to derive from both, but in *Cochlospermum* the main root seems to be principally
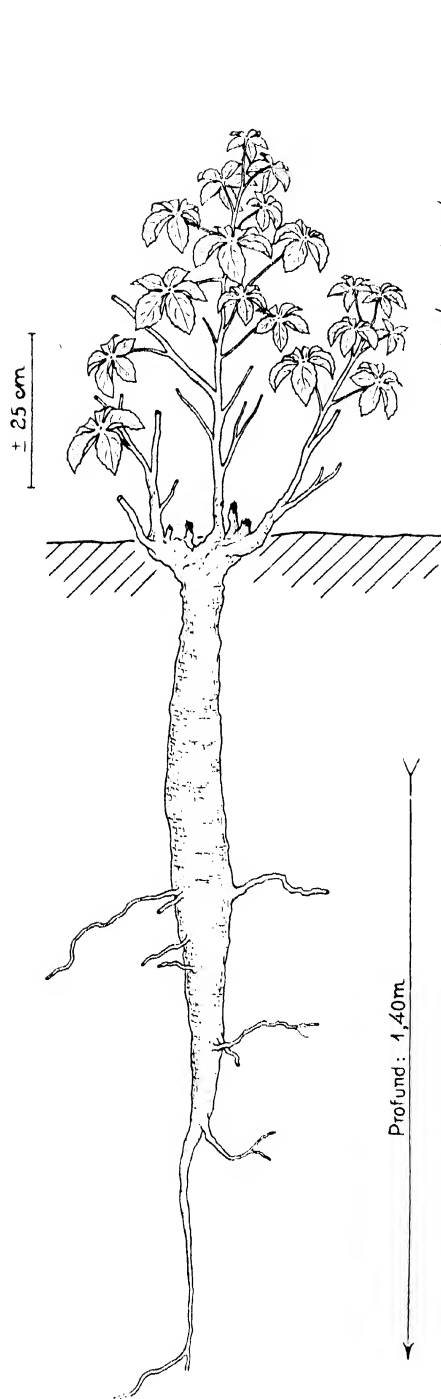
Fig. 26. *Cochlospermum insigne* (27 January 1946);
after M. Rachid.
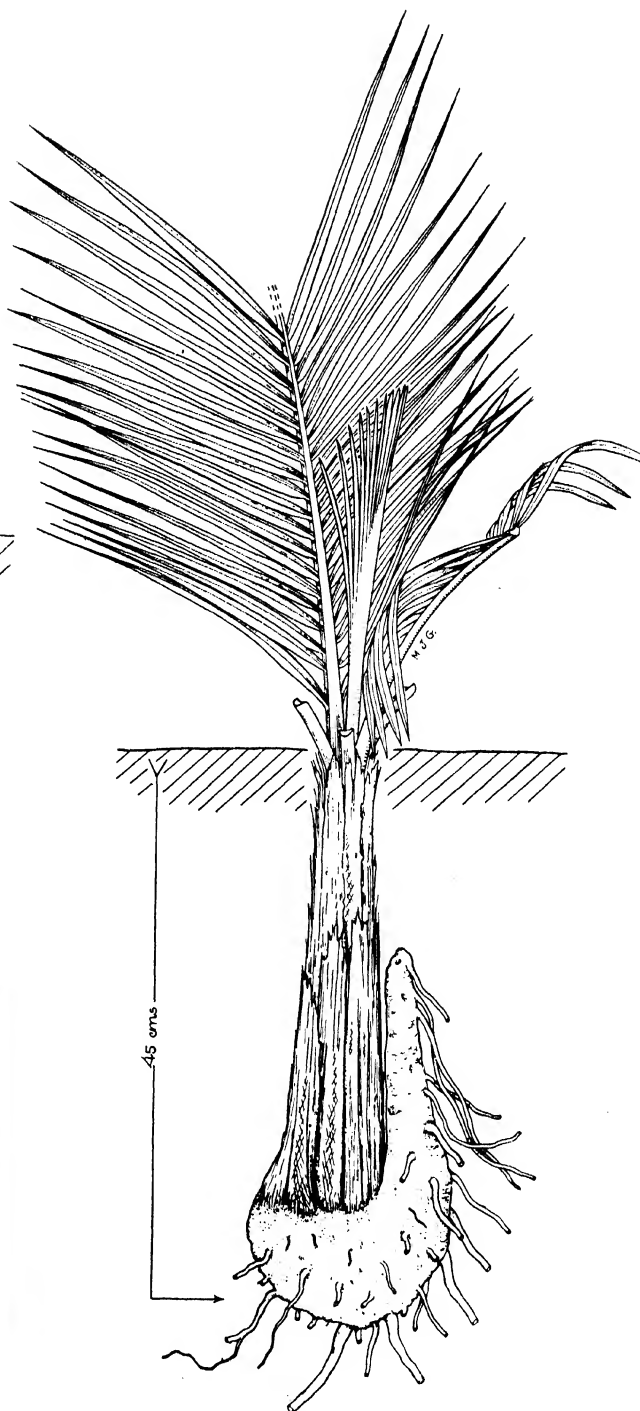
Fig. 27. *Attalea exigua* Drude, showing the subterranean stem;
after Rawitscher and M. Rachid (1946).
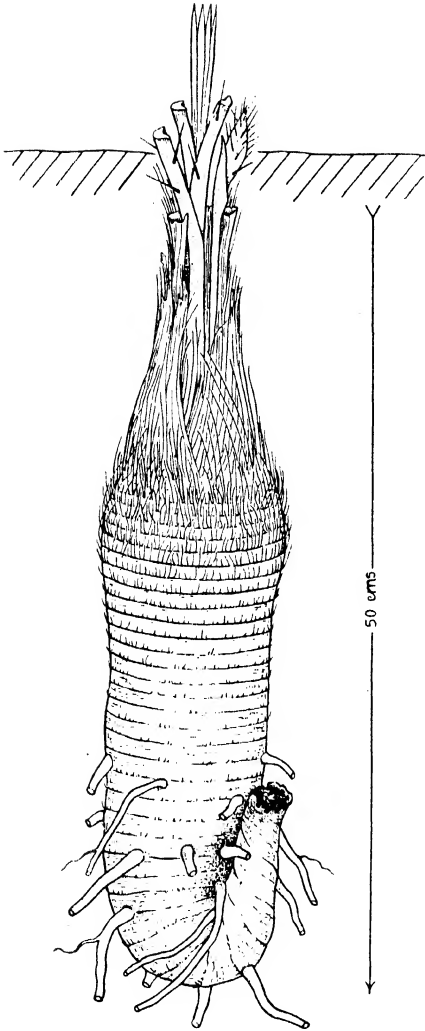
Fig. 28. Subterranean stem of *Acanthococos*
sp., adult specimen; after Rawitscher and
Rachid.
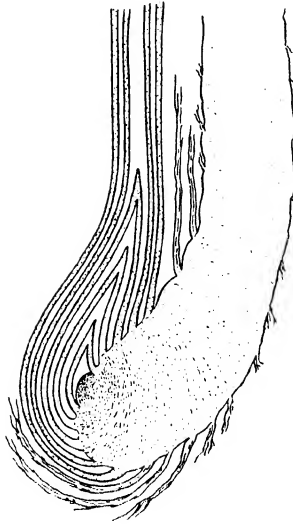
Fig. 29. Subterranean part of a
younger specimen of *Acantho-
cocos* sp., the growing point
beginning to turn upward; after
Rawitscher and M. Rachid.
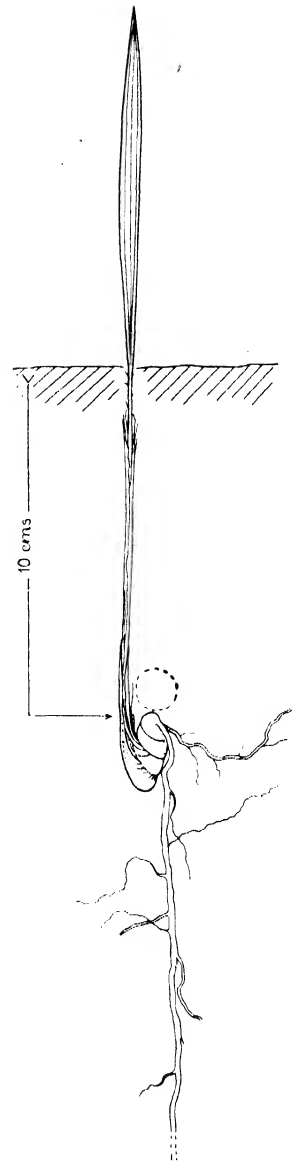
Fig. 30. Seedling of *Acanthococos*
sp.; the interrupted circle indi-
cates the position of the seed.

involved. Determinations of water content in the latter gave 78% in January, and 75% in September at the end of the dry period. Protection against loss of water in the dry soil seems to be very good.

Very interesting also are the subterranean trunks of certain stemless palms; their existence is known already for *Attalea exigua* (Fig. 27), frequent in pastures and range lands, and not characteristic of the Campo Cerrado. In this M. Rachid found another species, as yet undetermined, of the genus *Acanthococos*, where she could follow the interesting development of the subterranean part. Figs. 28–30 show how the growth of the stem, after germination, is directed at first vertically downwards; only the leaves show negative geotropism. When a depth of 50–60 cm. is reached, the growing point initiates a 180° curvature. The early stages of the stem disappear, and finally only the thicker, upward growing part of the trunk is left (Figs. 27, 28). This takes several years, and only now the palm produces its inflorescences just above ground. The roots, which derive from
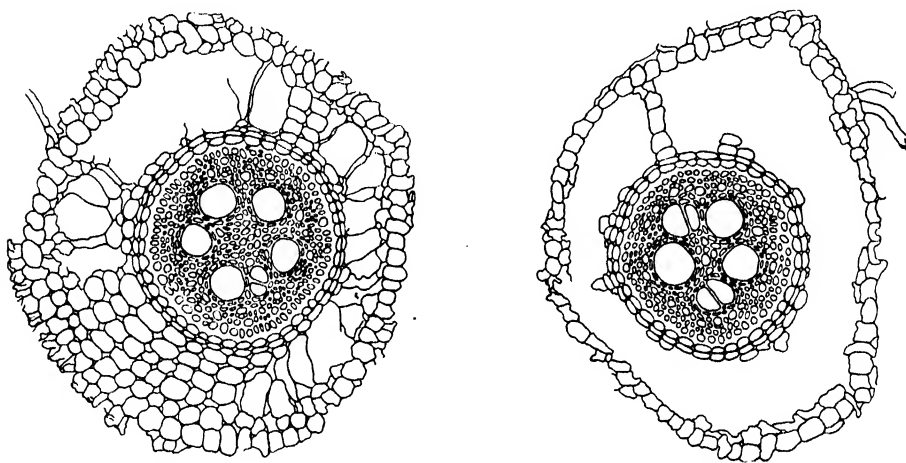
Fig. 31. Transverse section of two roots of *Panicum spectabile*. The cortical parenchyma at the beginning (left), and at the end of decomposition.

the subterranean stem, were generally found, like those in *Cochlospermum*, in the upper 2 m. A similar case has been described and figured for *Sabal mexicana* by Martius (1823–50).*

A group that shows no evident protection is the grasses, the most frequent and important species being *Echinolaena inflexa*, which, however, is common also in other associations than the Campos Cerrados. Its roots penetrate to 1–1·5 m., its stomatal mechanism is not very efficient, and when the water in the soil becomes scarce the leaves dry up, although some growing-points and some minute leaves always persist alive until the spring. The behaviour of this grass seems to be in accordance with Miss Henrici's (1927) statements for grasses from South Africa. One significant feature of the roots, described by Goossens (1935, see also Henrici, 1929) and mentioned by Walter (1939) for African grasses, was encountered similarly in several Brazilian species, i.e. the development of a sheath that involves the central cylinders. In these the parenchyma of the cortex disintegrates, leaving a hollow space between epi- and endodermis. This isolation may constitute a protection against suction forces developed by drying soils; ecologically it is important, because so many canals existing in the soil form an easy passage way for percolating water.

* See also Bondar (1942).

We may add that as a rule in Cerrado land permeability to water is extremely great. Even the heaviest tropical rains are absorbed immediately, without formation of puddles or a superficial overflow of water, whereas roads which cross the fields, on the contrary, are transformed into real streams.

5. CONCLUDING REMARKS

For lack of space we cannot enter into a detailed discussion of the conclusions which can be drawn from the foregoing observations. Their bearings, in part, are of an agricultural and silvicultural order. But as we started with the question, asked by Lund, about the real climax of the region, we may sum up as follows.

The abundance of water encountered throughout the year in the deeper part of the soil, together with the fact that the transpiration even in the driest time of the rainless period is not greatly diminished, leads to the conclusion that indeed the true climax, at least at Emas, is not the Cerrado vegetation but one of a more forest-like character. This agrees with the fact that, even in the drier interior of the State of São Paulo, there exist continuous virgin forests of a rather hygrophilic character which have not yet been reached by colonization, i.e. destruction. These forests never use up entirely the water stored in the soil, so that rivers and streams here flow throughout the year. This is different in the drier parts of Brazil. Already in northern Minas the still hygrophilous forests consume in the dry period all their water reserves, streams and rivers drying up annually (Silveira, 1923). Progressing from here to the still drier north and north-east we come to the region where the Cerrado is at its best and where it must be considered as a climax. We must suppose, that migrating from here it has invaded the clearings opened by deforestation.

Often treelessness is attributed—in Brazil as in many other countries—not to the scarcity of water, but to edaphic factors such as sterility or impermeability. That such arguments are unsustainable for the case of Emas can be demonstrated from the fact (p. 240) that fire-protected areas at Emas (as at Lagoa Santa) can be brough tto bear a dense tree-cover. But even where reforestation to-day meets with edaphic difficulties we must not forget that the qualities of the soil are variable and depend greatly upon lixiviation. This—extremely heavy in humid tropical conditions—begins or increases rapidly after felling the virgin forest, and especially if agricultural methods introduced from the temperate climates are applied indiscriminately—the degradation can be so strong that artificial or natural reforestation seems nearly impossible (Rawitscher, 1946). Nevertheless, the climax vegetation would still be the primary virgin forest.

6. SUMMARY

Campos Cerrados of a savanna-like aspect cover extensive areas of central and southern Brazil; they are known especially from Warming's floristic descriptions of Lagoa Santa. The question whether the existence of their stunted and poor vegetation must be ascribed to the dryness of the climate, or to human interference, especially the annual burnings, has been much discussed; it can be resolved only by examination of the water economy of these Campos. This was the aim of the research work here related, undertaken in the Campos Cerrados of Emas—Pirassununga, near São Paulo.

The depth of the soils, as usual under humid-hot conditions, is very great; a continuous underground water level occurs at 17–18 m. Drought at the rainless period enters

only the top layers to 2 or $2\frac{1}{2}$ m. Beneath, the soil contains the humidity stored from the rainy period; it is always wet and excess water drains off all the year around.

The behaviour of the vegetation depends on whether the roots reach the always humid part of the soil or not. The first is the case of the majority of the small trees and shrubs; they often maintain their foliage during the dry season, and transpiration values, examined by means of rapid weighing, infiltration, etc., were always high. Saturation deficit of the leaves remains low, and the stomatal mechanism in these plants as a rule reacts slowly. They have no xerophytic character.

The shallow-rooted part of the vegetation is composed of grasses which wilt when the drought reaches the depth of their root system (*Echinolaena inflexa* about 1·50 m.), or summer-green plants, that generally are perennial, but survive in the dry season only in the form of subterranean bulbs, 'xylopodia' or even very great root or stem-formations, such as the 'subterranean trunks' of *Cochlospermum*. In the wet season the top-layers of the soil are generally humid, so that these plants too transpire rather freely, without developing great water deficits of the leaves. Their stomatal reactions are more active than those of the deep-rooted plants, but in rapidity they are behind those of the leaves of high forest trees, as the comparison with *Cedrela* and *Copaifera* shows. The summer-green part of the vegetation may be compared in this respect with the tropophytic, mesophytic plants of temperate climates.

The abundance of water in the soil of Emas and the fact that in undisturbed areas under similar conditions there still exist forests of a rather hygrophytic character, lead to the conclusion that the Cerrado at Emas is not the natural vegetation of this region, but a fire-climax. The natural development centre of these formations must be sought in the drier parts of Brazil, from whence they may have migrated after the clearing of the forests, and successive deterioration, abandonment and periodical burning of the land.

The vast extension of to-day's infertile Cerrado land must be ascribed to the application of agricultural and silvicultural methods introduced from the temperate climates, which, under tropical-humid conditions, endanger the fertility of the soils.

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A PORTABLE ALTERNATING CURRENT BRIDGE AND ITS USE FOR MICRO-CLIMATIC TEMPERATURE AND HUMIDITY MEASUREMENTS

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(With Plate 21 and five Figures in the Text)

The need is often felt, in micro-climatic studies, for measuring instruments suitable for the investigations planned. In general, it may be said that in order to be suitable for the greatest number of purposes, measuring instruments must be portable and capable of registering temperature and air humidity in the smallest possible area, and this must not be effected at the expense of the accuracy of the measurement or cause any disturbance to the micro-climate. The functioning of electrical measuring instruments must be independent of current from the public electricity supply. These requirements are met satisfactorily by thermocouples for temperature measurement, but operations in the field are hampered by the great sensitivity of the galvanometer to shocks, and by the fact that it is necessary to have a definite reference junction.

Micro-climatic measurement of air humidity is more difficult. A great step forward was made with the Sulphuric Acid Hygrometer (Nielsen & Thamdrup, 1939), by which air humidity can be registered in very small areas. A small self-registering thermo-hygrograph, which has proved very suitable for micro-climatic measurements, was constructed by Krogh (1940). It registers the temperature by a small spring of bimetal, and humidity by means of a short hair.

In the hope of finding methods more suitable for micro-climatic measurements in the field and for laboratory experiments than those already in existence, the author has for some years conducted occasional experiments with feeling units to measure temperature and air humidity in conjunction with a portable alternating current bridge. The bridge and the resultant types of feeling units are described. The units are mainly made of platinum wire and glass tubes of various thicknesses, and with a little handiness they can be made by using a Bunsen burner with a very small flame so that dimensions and shapes may be varied to a certain degree to meet any special requirements. Practical hints for treatment of platinum and glass may be found, for instance, in Ostwald-Luther (1931).

THE BRIDGE

The main constructional features of the measuring bridge will appear from the diagram in Fig. 1 and Pl. 21. An alternating current is produced by a reed-type audio oscillator (in the top left-hand corner of Pl. 21). For this oscillator a Philips's type KC3 electron tube, with a filament voltage of 2 V. (3 V. battery with a resistance) and an anode voltage of 60 V., has been used. Alternating current is necessary in measuring resistance of electrolytes to prevent polarization and to allow the use of headphones instead of a galvanometer. The current is conducted to a Wheatstone bridge in which two adjustable resistances with different measuring ranges may be included by means of a change-over switch. One of these resistances consists of five dials, which permit measurements from 1 MΩ ($10^6\,\Omega$) down
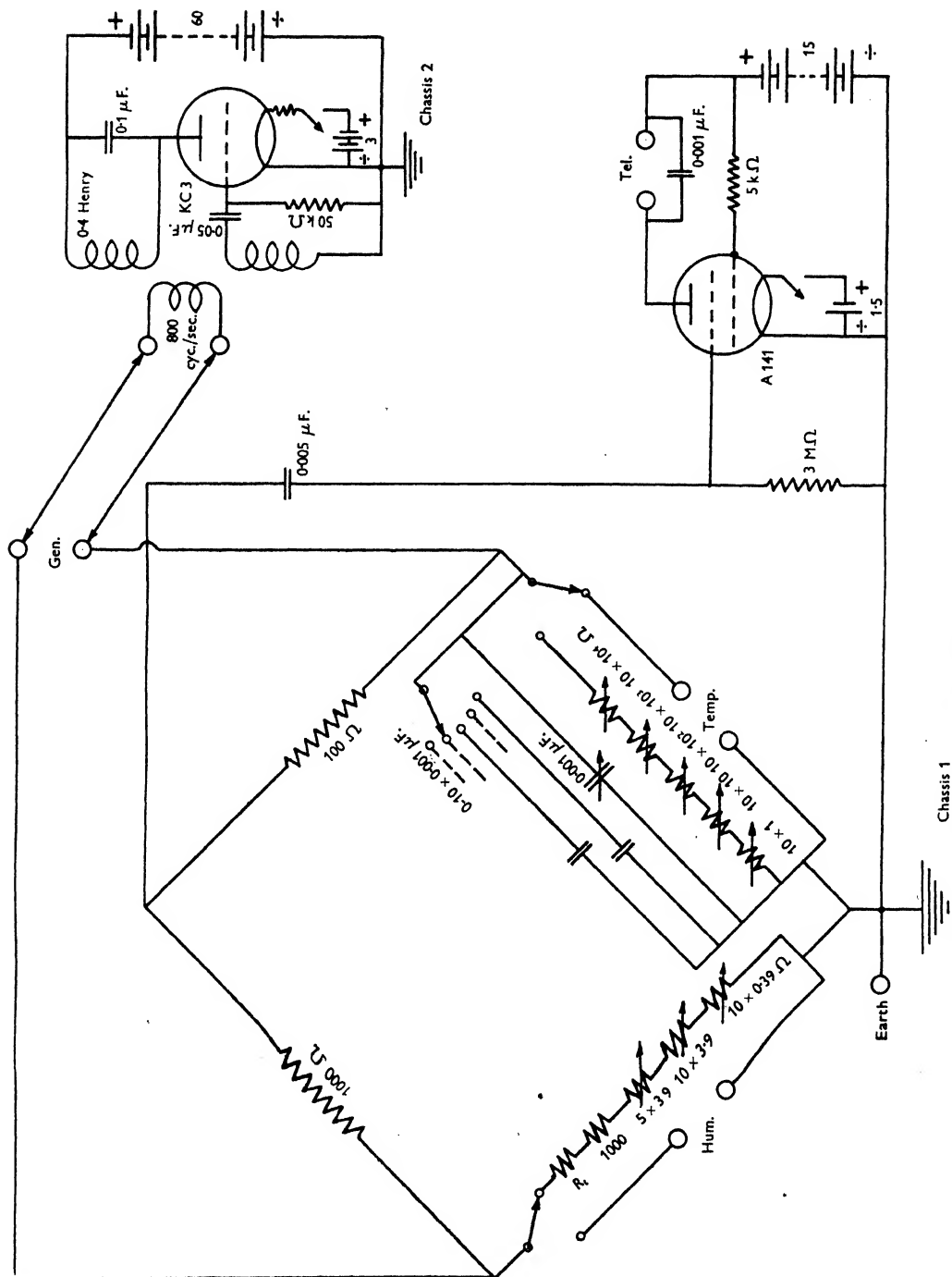
Fig. 1. The alternating current-bridge diagram. (Tel. = Headphones.)
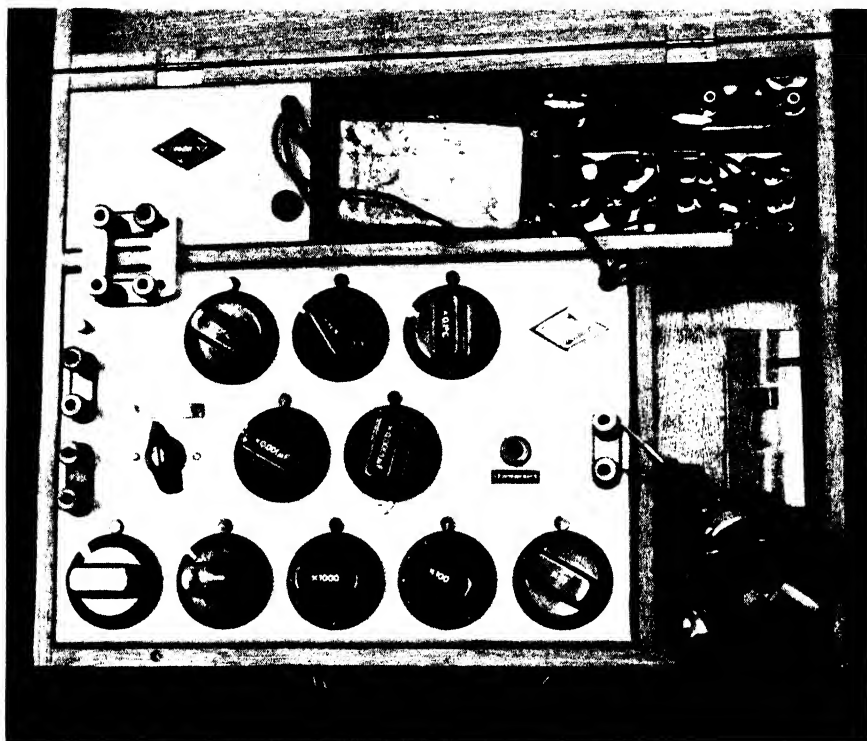
A photograph of the alternating current bridge.

to 1000 Ω, with an inaccuracy not exceeding 3 per mille. The accuracy decreases for lower resistances. Greater resistances may be measured by including a shunt (1 MΩ). The other variable resistance is intended to measure temperatures, and will be dealt with later. When measuring, the dial resistances are changed until the bridge is in equilibrium, which will be the case when the tone produced by the alternating current has disappeared in the headphones, and it is now possible to read the resistance direct from the dials, if no shunt has been included.

A frequency of 800 Hz. has been preferred because the human ear is most sensitive at this range, but it is necessary to interpose a one-step amplifier because an alternating voltage of under 2 V. can then be used, thereby reducing the heating of the feeling units to a minimum. A double grid tube (Philips's type A 141) with 1·5 V. filament voltage and 15 V. anode voltage has been used.

It is, however, not always possible to obtain complete silence in the headphones by merely balancing the bridge for ohm resistance. It is also necessary to balance for capacity resistance. This is effected by Schering's Method in the two centre-dials. By means of these it is possible to interpose up to 0·01 μF., which will suffice for most measurements. For the lowest ohm resistances, where the capacity resistance is highest, another condenser will have to be connected in parallel, with a capacity of 0·1 μF.

The audio oscillator and the bridge with amplifier are placed in separate sections of a wooden box and built-in in iron boxes for screening. The current is supplied by four dry batteries placed in the back compartment, and a fourth compartment is used for the headphones and feelers. The consumption of current is very small, so that only with very frequent use need the batteries be replaced more than once a year. The dimensions of the box are $50 \times 39 \times 15$ cm., and the weight, including batteries, is 14 kg., but it may be reduced somewhat by using aluminium instead of iron, and the size can also be reduced. The apparatus is so robust that it has been forwarded unwrapped by parcel post without having suffered any damage.

Instead of using the headphones to balance the bridge, a 'magic eye' may be used. This will be convenient for laboratory use, but it is unsatisfactory for use in the field, because it involves a considerable increase in current consumption and amplification, and is difficult to read off in sunlight.

MEASUREMENT OF TEMPERATURE

Resistance thermometer. The topmost three dials of the bridge are intended for measuring temperatures. The resistance has been adapted so as to allow the temperature to be read off directly from the scale, if resistance thermometers of platinum with a resistance of 100 Ω of the kind available in the shops are used.

The range is from 0 to 61° C., but may be changed by altering the resistances in the bridge, and it may be increased by 50° by merely inserting five more resistances of 39 Ω (see Fig. 1). The measuring accuracy is one-tenth of 1° C.

The measuring bridge may be used to measure temperatures of a wider range than indicated in the 'scale' by using—instead of a resistance thermometer of 100 Ω—a platinum wire with a lower resistance and interposing a resistance which is independent of temperatures, but only at the expense of the measuring accuracy, the latter being diminished in proportion with the reduction of the resistance of the platinum wire. If the resistance is say about 80 Ω, the measuring accuracy will be ½° C.

By using a very thin resistance wire of platinum one advantage will be achieved which is not possible to the same degree in other types of thermometers. The measuring will be practically independent of radiation, so that even in the most glaring sunlight it will be possible to measure the true air temperature without having to make shading arrangements that may cause disturbances in the micro-climate. By using a resistance wire of 0·02 mm. diameter the maximum heat effect caused by radiation will be 0·14° C. (central Europe, Albrecht, 1927). A wire of 0·03 mm. may be heated to 0·20° above air temperature. It is much less fragile than the thin wire and is, therefore, easier to handle and considerably cheaper, but it must be 2·25 times as long to afford a corresponding resistance.

A resistance thermometer where the length of the platinum wire, and consequently the resistance, may be varied, is shown in Fig. 2. In an ebony handle are placed two bent metal bars which may be connected to the wires which are carried through a hole at the other end of the handle and connected to the bridge. At the end of each of these metal bars is a fine slit in which is fixed a platinum wire of about 20μ thickness; they may, how-ever, also be fitted with small terminal screws which will facilitate the fixing of the platinum wire. Between the above-mentioned two metal bars, but at a higher level, is placed a third, longer metal bar, which is adjustable and may be fixed by a screw. This bar is also bent, but at the apex it is provided with a tiny hook, round which the platinum wire is
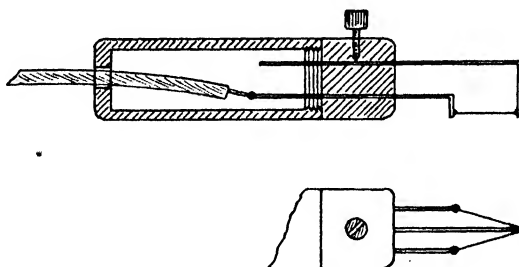
Fig. 2. The resistance thermometer.

looped. The bar is pulled cautiously out until the wire has been straightened without being too tight, as it will very easily snap. Consequently, the platinum wire will assume a V-shape, and the angle may be varied by turning the two metal bars (which form the electrodes) to the sides. The V-shape renders it possible to undertake measurements with a platinum wire of given length within a smaller area than would be possible if the wire were straight (and there is naturally nothing to prevent the wire from being folded several times).

A home-made thermometer, which is independent of radiation, may be made by using a glass tube instead of an ebony handle. To the inside end of the tube are fastened (by melting or otherwise) two platinum electrodes (of say 0·2 mm. diameter), which at one end are connected to the wires carried through the handle. The other ends of the electrodes project beyond the handle and are connected to the resistance wire which is sensitive to temperature change. This may be effected by welding over a slow-burning flame of the Bunsen burner. To obtain a V-shaped resistance wire it is recommended to use a tube with a narrow bore and to fasten the electrodes to the outer side and carry a sliding stick through the bore. After mounting the resistance wire it may be secured by immersion into molten glass putty together with the upper end of the handle, should that be made of material unsuitable for melting on to glass.

As the measuring bridge in question is built for the range from 100 to 123 Ω, a pre-resistance which is independent of temperatures must be inserted. Such a pre-resistance may be made by winding a resistance wire of manganin round a short glass tube, fastening it, and immersing the tube into a solution of shellac in alcohol. To prevent the resistance from changing later, it must be left in a thermostat for 24 hr. at about 135° C. It may be placed in the hollow handle.

If it is not imperative to obtain the maximum accuracy obtainable ($\frac{1}{10}$° C., which requires a platinum wire of about 27 cm. length at 20 μ thickness), the adjustment of the resistance is easy. If an accuracy of say $\frac{1}{5}$° is sufficient, the resistance will cover a range of $5 \times 61° = 305°$ and as a larger interval than one-quarter of this, i.e. 76°, will hardly ever be required, the variation of the resistance in this case will barely be 6 Ω, within the 23 Ω available. The provisional adjustment may be made by means of the other rheostat ('humidity'). The mounted and (possibly) lacquered platinum wire may be adjusted by immersion into water of known temperature, for instance, ice-water and boiling water, upon which the corresponding positions of the dials are read off. No further measurings of temperatures are necessary as the temperature is a rectilinear function of the resistance. If the resistance of the platinum wire is known at a given temperature, it is possible to calculate the resistance at other temperatures. The temperature coefficient of platinum is 0·0039.

The effect of the resistance thermometer on the micro-climate is infinitesimal. The temperature of the metal bars holding the platinum wire will only be appreciable through their heating (or cooling) of the air. Their radiation is naturally even smaller than that of the sun, and there is no heat conduction of any consequence out to the thin platinum wire. Moreover, the thermometer need only be placed at the place of measuring during the very short time required for adjustment to silence, as it will immediately assume the temperature of the surroundings. This will normally be an advantage, but may be embarrassing where temperatures vary very quickly. In that case the limits of the variations in temperature may be found by adjusting to the highest and lowest points where silence may be obtained for short periods.

If an accuracy of more than 1° C. is not required, and in the majority of cases this will undoubtedly be sufficient for micro-climatic measurements, the total length of the platinum wire must be about 27 mm.; it will then be possible to measure the temperature at a definite level and within a very small area. The surface temperature of the soil may also be measured by cautiously letting the lacquered platinum wire touch the substratum which, to give a couple of examples, may be of importance in the study of the ecology of epiphytes and epiliths, and of effects of radiation and transpiration on the leaf temperatures and temperature preferences of small animals.

Electrolytic thermometer. The resistance thermometer described in the foregoing can only be used in dense vegetation, when the thin platinum wire is protected against molestation. The measuring bridge, however, can be used for another type of thermometer which has proved extremely useful in such conditions if, like mercury thermometers, it is protected by shading against radiation. The principle is identical with that used in radio sounding for registration of temperatures in the upper strata of the atmosphere (Harmantas, 1941), as the dependence on temperature of the conductive capacity of electrolytes is applied. For most electrolytes the resistance is reduced by 2–$2\frac{1}{2}$% for 1° C. rise in temperature, so that by means of the measuring bridge it is possible to register differences in temperature of less than one-fifth of 1° C.

Very small quick-action thermometers of this type have been produced of capillary tubes in the following manner (Fig. 3). The capillary tube is given a sharp bend, but so that its bore is retained, and in the bend is made a small hole just big enough to allow a platinum wire of 0·2 mm. thickness to be put into the tube. The hole is made by holding the capillary tube just outside the small flame of a Bunsen burner and pushing the platinum wire through the flame. By pricking the capillary tube a few times a hole will be made without any damage to the tube, because the glass is only melted in the immediate vicinity of the heat-conducting platinum wire. The thin glass layer which has been deposited at the end of the platinum wire is now removed, and the wire is put through the hole. The most difficult process will now be that of making an airtight join between the platinum wire and the glass without closing the capillary tube. If the platinum wire be put in without first making a hole it will be covered by a thin layer of glass, and consequently it cannot be used as an electrode. The melting-up of the hole will be considerably facilitated by previously placing a glass droplet on the platinum wire (preferably of glass with a comparatively low melting-point which will easily fuse with other kinds of glass).
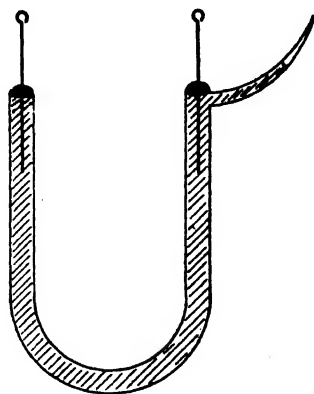
Fig. 3. The electrolytic thermometer (slightly diagrammatic).

Capillary tubes of Jena-glass have been used, and the droplet has been made by putting the platinum wire into a capillary tube, which at its point was melted on to the platinum wire, after which the rest of the capillary tube has been broken off. By heating cautiously with a small gas flame the droplet may be melted to the capillary tube so sealing the hole.

On one side of the platinum wire the capillary tube is pulled out into a thin point, and may be bent upwards as shown in the illustration. The other end is bent into a U-shape and cut off level with the platinum electrode which has been melted on; now the other electrode is melted on.

The capillary tube is now placed in a bowl with the electrolyte which is boiled a few times, thus expelling all air and filling the tube with the electrolyte. The fluid in the outer part of the tube is evaporated, or the tube is taken up just before it is completely filled in order to avoid concentration differences, and the point is sealed up as quickly as possible by putting it into the flame. If it is kept there too long, the steam pressure will cause a bubble to form which will burst. In the course of time some of the fluid will enter the narrow part so that an air-bubble will form between the bend and the point of the capillary tube, but it will not enter the U-tube, which must be completely filled in order to prevent the shifting air-bubble from changing the resistance.

Adjustment should not be made until after a few days to counterbalance any concentration differences and to ascertain that the tube is absolutely tight.

In adjusting electrolyte thermometers it should be remembered that the resistance of the electrolytes is not a linear function of the temperature. It is, therefore, necessary to mark at least three points to be able to draw the curve from which the temperature is read on the basis of the resistance. For practical reasons an electrolyte concentration will be preferable which does not give too low a resistance, for instance about 20,000, partly in order to utilize the sensitivity of the apparatus, and partly because high resistance

corresponds to a comparatively low capacity, so that it will only be necessary to use the two buttons for the compensation. On the other hand, the resistance should not be unnecessarily high, lest extra-electrolytic conduction and soluble particles of the glass should interfere.

The electrolyte thermometers described above can be used under conditions where frequent reading of mercury thermometers would be difficult, for instance, dug into the earth, on trees, or in enclosed spaces. By carrying the wires from the various thermometers to a switchboard it is possible from the same place to listen in to the resistances and read the temperatures from the curves of the individual thermometers.

In comparison with thermocouples, which, incidentally, have other advantages, the above-described departures distinguish themselves by making it possible to use the same measuring bridge as in humidity measurements, and besides, the latter is more robust than the ordinary type of apparatus for measurement of thermo-electricity, and therefore better suited for use in the field. Further, no standard reference junction is required.

If an electrolyte thermometer is not intended to react to quick changes in temperature, for instance, in soil, it may be protected by melting it into a block of paraffin wax.

Instead of electrolytes it is possible, in conjunction with the bridge, to use uranium oxide, which has a similar dependence on temperatures. It is this substance that is used in the so-called 'thermisters' which are available commercially.

HUMIDITY MEASUREMENT

Dewpoint hygrometer. A small hygrometer with electrical registration of the dewpoint can be made in the following manner. For the hygrometer vessel a small glass container is used. For the thermometer is used a platinum wire of 0·02 or 0·03 mm. thickness, each end of which is welded on to a thicker platinum electrode. These are melted on to the sides of the glass, and the resistance wire is wound in a spiral up round the lower half of the glass, while the latter is being heated just sufficiently to make the wire stick. This may be done by weighting the resistance wire slightly, while the glass, held a little obliquely, is turned slowly over a gas flame.

Fig. 4. The dewpoint hygrometer (slightly diagrammatic).

The resistance wire will not stand the heat of the gas flame unless it is in contact with, or very close to, the glass. A manganin resistance may be interposed if necessary, and the platinum wire used as a thermometer in conjunction with the measuring bridge in the same way as the radiation-independent thermometer mentioned earlier.

Between the coils of the resistance wire is wound another platinum wire (0·03 or 0·05 mm.), which at the top is fixed to a third melted-in platinum electrode, while the lower end is dead. The hygrometer should be mounted on an ebony block and be protected by an open-meshed wire-netting.

When the glass tube has adapted itself to the surrounding temperature, the latter is measured, and ether is poured in by means of a pipette. A long, angle-bent capillary tube is put down into the glass tube, and air is blown through it by mouth until the temperature has fallen to the dewpoint.

The third electrode is intended for exact determination of the dewpoint, as the third electrode, together with one of the thermometer electrodes, is connected to 'humidity'.

The resistance on the surface of the glass, which is originally extremely high, will gradually decrease when the dew begins to settle. This principle (without resistance thermometer) has previously been used by Reed (1941), but it was necessary to determine by calibration by chemical means at what resistance the dewpoint was reached. It has, however, been possible to find a procedure in which the dewpoint can be determined with very great accuracy. The entire hygrometer, with the platinum wires mounted on to it, is immersed into a silver-plating bath (see below), but the silver plating is interrupted at a stage where, in transparent light, the silver coating appears as a brownish coating, and the hygrometer is then washed. The silver has now been precipitated in the shape of very fine grains very close to each other, without having appreciably increased the conduction at the surface of the glass, but instantly, when the dew settles on the glass, a connexion is established between the silver particles, and the resistance decreases sharply. When the resistance increases again, a switch-over is made at once to the temperature measuring. The resistance on the surface of the glass is (just below the dewpoint temperature) big enough to have no influence whatever on the temperature measurements, provided that the silver plating has not proceeded too far. If the thermometer wire has a resistance of $100\,\Omega$, a relatively small resistance on the glass surface (as low as $1\,M\Omega$), will cause the result to be $0.01\,\Omega$ too low, equal to $\frac{1}{30}°$ C.

The silver plating may be carried out in the following manner (Ostwald-Luther, 1931, p. 331): add NH_4OH to a 1% solution of $AgNO_3$ until the precipitate first formed is nearly dissolved. To 200 ml. of boiling water add 0.4 g. $AgNO_3$ and 0.38 g. of potassium sodium tartrate (Seignette's salt), both dissolved in a little water. Boiling is continued for about half an hour, and the precipitate is strained off. The solutions will keep for a long time. Before use, they are mixed in equal proportion (1/1) in a glass into which the hygrometer is immersed. The treatment may be repeated, and the silver may be removed, if desired, by immersion into nitric acid. It is not necessary to clean the glass in advance.

The described hygrometer has several advantages for ecologic measurements, and undoubtedly for other purposes as well, in comparison with those normally used.

It may be made very small. The thermometer has been placed in the very spot where the dew settles and immediately assumes the temperature of the surface. Electrical registration of the formation of dew is more sensitive than visual, and may, like registration of temperature, be made at a distance so that the operator will not influence the result by his own breathing and radiation of heat, and it makes it possible for the registration to be made in places where the hygrometer is hidden, for instance, in dense vegetation. The measurement itself may take place at such a distance as the capillary tube for the air passage will allow, and the capillary tube may advantageously be extended by a thin hose. If the capillary tube is carried through a rubber stopper in which there is also a tube for the outlet of air and ether vapours, the influence of the hygrometer on the micro-climate will be minimal.

Resistance hygrometer. Exact measurement of the relative air humidity has always caused difficulty, especially in the case of high air humidity. At a relative humidity of over 95% the two most commonly used methods, the hair hygrometer and the psychrometer are very inaccurate, and their use in micro-climatic measurements will especially cause uncertainty, the hair hygrometers in particular on account of their considerable

size, and the psychrometer because an air current must pass the wet-bulb thermometer, rendering a mixture of the air masses inevitable.

If it were possible to design a hygrometer with which relative humidities between 95 and 100 % could be measured with great accuracy, it would be possible to measure the force with which water is held in soil, and which consequently has to be overcome by the roots of plants in water uptake. There is a definite relation between the suction force of soil and the relative humidity in the cavities of the soil, and so also with the vapour pressure. A relative humidity of 99 % corresponds to a suction force of 13 atm., 98 % to 26 atm., 90 % to 136 atm., etc., a relationship only slightly dependent on temperature (Shull, 1939).

Measurement of the suction force of the soil may be made in the laboratory, where a constant temperature may be kept, by comparing the vapour pressure above solutions of varying concentrations placed in small capillary tubes above the soil in an airtight vessel (Ursprung & Blum, 1930). A registration of the soil moisture tension under field conditions, would, however, be of great scientific as well as practical importance, and it was in the hope of developing a method whereby this could be attained that the experiments with the resistance hygrometer were begun. When foreign literature became available again after the war, it was found that the problem had been investigated, particularly in the United States, and various methods had been adopted (see Kelley, Hunter, Haise & Hobbs, 1946; and Slater & Bryant, 1946). In one of the methods, moisture measurements depend upon determination of the electrical resistance between two electrodes embedded in a block of gypsum which is in moisture equilibrium with the soil (Bouyoucos & Mick, 1940). These measurements may be made with the Wheatstone bridge described here. With the gypsum blocks one may measure suction forces between 1 and 15 atm., although with considerable uncertainty at the highest suction force. This, and other methods, have already proved important in investigations of water economy in irrigated areas.

In the method used by the author to measure the relative humidity of air, the hygroscopicity of glass-wool is applied. The quantity of water adsorbed by glass-wool depends on the relative humidity of air (McHaffie & Lehner, 1925) and is only dependent on temperature to a very small degree (Wadsworth, 1944). To a definite quantity of adsorbed water there corresponds a definite resistance on the surface of the glass-wool, but the resistance also depends on the temperature, as set out in greater detail below.

Other materials than glass-wool have also been tested (asbestos, cellulose, silica gel), but they have proved unstable or to have other shortcomings.

Among the various methods tested of mounting the glass-wool, the following has proved the most suitable. Two platinum wires (for instance, 0·05 mm. in diameter) are welded on to thicker platinum electrodes which are melted on near one end of a short glass tube (for instance, 4 × 0·6 cm.). A small bunch of fine glass-wool (Merck), of the length of the glass tube, is distributed around the tube, and one platinum wire is wound firmly round and melted on to the other end of the glass tube. The glass-wool may now be distributed more evenly with a needle so that it will form a thin coating outside the glass tube, and the other platinum wire is wound round the glass tube in
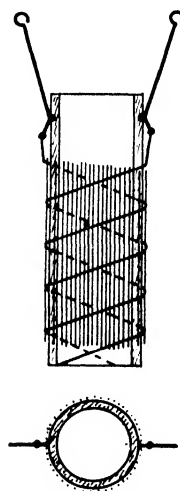
Fig. 5. The resistance hygrometer (slightly diagrammatic).

the same manner as the first. The resistance of the glass-wool is measured between the two electrodes. The hygrometer is sensitive to handling, and, like the dewpoint thermometer, it should be mounted on an ebony holder, but even fairly rough shocks will not cause any shifting of the glass-wool and consequent changes of the resistance.

A small resistance thermometer may be constructed, as described in the dewpoint hygrometer, by winding the resistance wire round a thin glass tube which is put into the bore of the glass tube to which the glass-wool has been fastened. A thermo-hygrometer of very small dimensions can thus be constructed. Knowledge of the temperature is not only a necessity for humidity measurements, but also indispensable for converting the relative humidity into other expressions for air humidity (for instance, by means of the nomograms by Gordon, 1940).

The resistance of glass-wool is very high in dry air, but suitable resistances may be obtained by winding the coils of the platinum wire very closely. The same effect may be achieved by using a thick layer of glass-wool, but longer time will then be required to obtain equilibrium with air humidity. The resistance may also be reduced by a previous treatment of the glass-wool with a weak solution of salt, and for this purpose KNO_3 has proved suitable, whereas the highly hygroscopic LiCl, which will greatly reduce the resistance, seems to gradually lose its effect.

When a dewpoint hygrometer is cooled down, it will surround itself with an air coating, in which the relative humidity will continue to increase until the dewpoint has been reached. In the same manner a hygrometer will be surrounded by a layer of air with too low relative humidity if it is warmer than the air to be measured. It will, therefore, be absolutely necessary to protect, not only the hygrometer, but also a piece of the wire, against radiation, lest the wire should conduct heat to the hygrometer (cf. Eggert, 1946). It is imperative to point out the importance of the hygrometer and the air having the same temperature, because this also applies to hair and sulphuric acid hygrometers, and this fact seems to be frequently overlooked by ecologists. In this way very considerable errors may arise, inasmuch as a difference of $1°$ C. is equal to about 5% relative humidity, or, expressed in terms of suction force, about 60 atm.

The glass-wool resistance varies greatly with the relative humidity, but is different for individual feelers and for low and high humidity. Between 70 and 100% relative humidity, the resistance for one feeler decreased by about 10% for a rise of 1% relative humidity, which means that with the bridge in question it is possible to register differences in relative humidity of about one-thirtieth of 1%. But this does certainly not mean that humidity can be measured as accurately as that, and generally that would also be immaterial.

To determine the efficiency of the hygrometer we have now the following issues: (1) To what extent are the measuring results reproducible? (2) To what extent does the resistance depend on temperature? (3) How long is required for the glass-wool to reach equilibrium with the water vapour of the air?

A solution of these three problems has been attempted by carrying wires to the bridge through an airtight rubber stopper. The latter is placed in a bottle so that the hygrometer is suspended above a solution of which the osmotic pressure is known, and thereby also the vapour pressure. The entire unit is placed under conditions of constant temperature.

This procedure does not give exact information about the time required by the hygrometer to adjust itself, because it cannot be known when the air in the bottle is saturated with the solution found in the bottle. If the hygrometer be put into a bottle that has been

left sealed for some time, it will immediately absorb moisture from the air above the fluid, thereby adjusting itself almost completely, but the ultimate adjustment can only take place according as the air becomes again saturated by diffusion from the fluid.

If the hygrometer be taken from damp air into drier air, the adjustment will be much slower. If no abrupt changes in the relative humidity are made, and the glass-wool coating is not too thick, the adjustment may be expected to take place quickly. At any rate, comparisons made with a hair hygrometer showed that the resistance hygrometer reacted with far greater rapidity to changes in the air humidity than the hair hygrometer; but it will not be possible, outside a closed space, to keep the humidity so constant that the changes will not always cause changes in the resistance of the hygrometer, and as far as the author knows, no apparatus exists that will react more quickly or sensitively to changes in the humidity and consequently a control becomes impossible.

The influence of temperature on the conductivity of glass-wool is rather considerable, and depends to some extent on the resistance. An increase in temperature of $1°$ C. has proved to reduce the resistance by $2\frac{1}{2}$–6%, which reduction is equal to between $\frac{1}{4}$ and $\frac{3}{4}\%$ relative humidity. It is, therefore, necessary to make temperature adjustments at several humidities, and to make correction curves in the manner followed by Bouyoucos & Mick (1940) in their gypsum block for examination of soil moisture. In this connexion it should be noted that the hair hygrometer is also dependent on temperature, as (according to Robitzsch, 1926) a difference of $4°$ C. at, for example, 80% relative humidity ($3°$ C. at 100%) from the adjusted temperature, will give an error of 1% relative humidity provided that the extension coefficient is the same as that of dry hair.

Even if the hygrometer be placed in an airtight bottle in equilibrium with the air humidity, the resistance will increase as soon as one approaches the hygrometer. This is undoubtedly due to the fact that the radiation from the body will cause a difference in temperature between the hygrometer and the air, and even a small difference will, therefore, give considerable errors in the temperature measurements.

After having made the resistance hygrometer, it is necessary to leave it for a few days in air saturated with moisture, as this has proved to cause a lasting change of the resistance, which would otherwise show incorrect results in measurements. This curious fact can probably be accounted for by the intense heat to which the glass-wool was exposed when the platinum wires were melted on.

When changing from damp to drier air, the adjustment will not only, as already mentioned, be slower than when going from dry to moist air, but the hygrometer will not reach quite the same resistance either. This hysteresis is common to all hygroscopic substances, but for glass-wool it is so small that it has not been discernible in ordinary microclimatic measurements. On the other hand, they must be taken into consideration in measurements of particular accuracy.

If the resistance hygrometer is to be used to determine the suction force of soil samples collected in the field, the samples are put into bottles instead of the mentioned salt solutions used for the calibration; the samples should be left under conditions of constant temperature, protected from radiation, and preferably in a water-bath from which the wires protrude so that the resistance measurements can be made without having to move the bottles. Both in calibration and in the actual measurements, the hygrometers must be air-dried for some time (several hours) before they are placed in the bottles.

For field measurements of the suction force of soil, the resistance hygrometers will hardly be so suitable as the Bouyoucos gypsum block at a suction force of less than 15 atm. (equal to about 99 % relative humidity). On the other hand, they can be used for higher suction forces where the gypsum block cannot be used. Besides, the resistance hygrometer has the advantage that it does not get into contact with the earth itself, so that it will not only register the suction force that is due to exsiccation, but the total suction force to be overcome by the roots of plants, and consequently also that which is due to salt content of the soil. In saline soil the resistance in the gypsum block will decline, although the relative humidity is lower, and consequently the result will be erroneous.

If measurements are to be made over a wide range of humidity, e.g. between 40 and 100 % relative humidity, it will be found most practical, on account of the great differences in resistance caused by the humidity, to have two hygrometers, each one specially intended for its own range.

The hygrometer may be used to measure very small amounts of water, when it is evenly distributed in an airtight, closed bottle of known cubic capacity, because it is possible when the temperature is known to calculate the amount of water per unit of air volume at a definite relative humidity. Experiments on this issue have not been made, but there can be no doubt that the method will be applicable, for instance, in transpiration experiments with small plants and animals. The amount by weight of water adsorbed by the glass-wool is quite insignificant; incidentally, it may be measured by quickly taking the hygrometer from a known relative humidity airtight to a bottle without any fluid and with a different known humidity and volume, e.g. room air. When equilibrium has been established it will be possible, on the basis of the relative humidity, to calculate the amount of water given off or consumed to equalize the difference.

From the description of the resistance hygrometer it will be understood that the calibration especially will cause the operation of it to take up some time, if its sensitivity is to be utilized to full advantage. The reproducibility of the results has turned out to be somewhat variable for the different hygrometers, but by careful handling they can measure the relative humidity more accurately than has been possible by other methods. Changes in the relative humidity are registered with rapidity and great sensitivity; other advantages are the small size, and the fact that they can be operated in small, closed spaces, which may even be separated by several metres from the measuring bridge. One hygrometer has been placed at 92 % relative humidity for 4 months without changing the resistance more than what corresponds to $< \frac{1}{2}$ % relative humidity, and Edlefsen (1933) has had the same experience when he used glass-wool to measure vapour pressure in a fixed arrangement in a thermostat.

Technically, there is nothing to prevent the different measurements dependent on changes in electrical resistances from being made self-registering so that several feelers are registered simultaneously. An instrument which will register automatically up to 72 temperatures has been constructed by a Norwegian physicist, but a detailed description of it has not yet been published.

In addition to the uses mentioned in the foregoing, the measuring bridge may be used to measure the conductivity of fluids. For this purpose Philips's 'dipping' electrode has been used, but other types can also be used. For measuring the amount of electrolyte in soil, four parts of distilled water to one part of soil are generally used. Further, the conductive capacity may be used to determine the salt concentration in sea water.

A table of the ratio between concentration and conductivity of sea water can be found in Thomas (1934).

SUMMARY

This is a description of an alternating current bridge built-in in a portable box with dry batteries for source of current supply. Resistance measurements of two different ranges can be made with it, one of which is narrow and intended for temperature measurements, and the other for resistance measurements of 10–$1,000,000\,\Omega$, or more. Four different types of feelers have been described, two for temperature measurements and two for humidity measurements, and these can be manufactured in the laboratory with platinum wire and glass tubes as the most important materials.

1. With a platinum wire of $0\cdot02$ mm. (or, as an alternative $0\cdot03$ mm.) thickness, air and surface temperatures may be measured with an accuracy of up to $\frac{1}{10}^{\circ}$ C. practically independently of radiation.

2. Electrolyte thermometers, or 'thermisters', are particularly suitable for measurements in inaccessible places, e.g. in soil, because readings may be made a long way off.

3. To determine the dewpoint a small glass tube is used, round which a resistance wire has been wound to measure the temperature. The dewpoint is determined by a sudden reduction in the resistance on the surface of the glass which has been given a thin silver coating. It is measured by condensate between the temperature wire and another platinum wire with a dead end.

4. A resistance hygrometer is made of glass-wool mounted outside a glass tube with two platinum wires. The resistance of the glass-wool between the platinum wires is measured. Besides being greatly dependent on the relative humidity of air it is also dependent on the temperature of air, which must be measured at the same time. Moreover, the measuring bridge may be used for a Bouyoucos gypsum block for continuous measurement of soil moisture under field conditions, and to measure the conductivity of fluids, and thus also salt concentrations in sea water.

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THE ECOLOGY OF THE CAIRNGORMS

PART 1. THE ENVIRONMENT AND THE ALTITUDINAL ZONATION OF THE VEGETATION

By ALEX. S. WATT, *Botany School, Cambridge* AND E. W. JONES, *School of Forestry, Oxford*

(*With plate 22 and eight Figures in the Text*)

CONTENTS

Tansley's *The British Islands and their Vegetation* (1939) presents the solid achievement of British ecologists. By implication it draws attention to the gaps in our knowledge, and in particular to our scanty information about the vegetation of the higher altitudes. For, apart from Price Evans's work on Cader Idris (1932), nothing has been done on the vegetation of the higher levels since the pioneer work of the Smiths (1900, 1904). The neglect had already been appreciated, and it was a desire to fill this gap that led to the organization of the Cambridge Botanical Expedition to the Cairngorms during short periods in the summers of 1938 and 1939.*

From headquarters at Glenmore Lodge (1150 ft.; 351 m.) the party made a study of the vegetation from about 2000 ft. (610 m.) upwards, on the series of spurs and valleys, plateaux, snow-beds and corries lying to the south and centred round the mountains of Cairn Gorm† and Cairn Lochan. This area is regarded by the senior author, who has walked

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* Initiated and led by Dr (now Professor) J. S. Turner until his departure for Melbourne in the summer of 1938 the expedition comprised the following, who, for different periods, assisted in 1938 or 1939 or in both years: M. Brown, N. A. Burges, H. Fletcher, R. Howles, J. Ingram, M. Ingram, E. W. Jones, J. B. Jones, G. Metcalfe, A. Richards, P. W. Richards, J. P. Riches, D. Simpson, A. Trueblood, J. Turner, D. H. Valentine, J. Valentine, S. M. Walters, E. F. Warburg, A. S. Watt, H. L. R. Whitehouse and B. Wilkinson.

† The spelling of place-names follows the one-inch Ordnance Survey Map.

over much of the Cairngorm area, as a fair sample of the physical features* and plant life of the Cairngorms as a whole.

Against this background of wider experience the present account serves as an introduction to a series of more detailed descriptions of the vegetation on the basis of broad altitudinal zones to be indicated later.

THE CAIRNGORMS

Geology and topography

The name Cairngorms, taken from Cairn Gorm itself, is in general use for the north-eastern spur of the Grampians lying between the rivers Dee to the south and Spey to the north-west (Fig. 1). The river Feshie (a tributary of the Spey) forms a natural western boundary. Eastwards, the height of the mountains gradually falls, and there is no natural feature forming a well-defined eastern limit, although the lower Glen Avon, Glen Builg and a line drawn south from them to the Dee may be recognized as a convenient boundary. The region bounded by these rivers includes all the high ground and the physical features characteristic of the group. Its area is approximately 20 miles by 12 (32 × 19 km.), and apart from the scanty population in the peripheral valleys the region is practically uninhabited and inaccessible, all journey into it having to be made on foot.

The central and larger part of this area consists of a mass of granite intruded through an old much-eroded peneplain of schists, gneiss and quartzites, lying at approximately 2400 ft. (732 m.). The granite forms an upper plane of denudation at approximately 3500 ft. (1067 m.), with four summits over 4000 ft. (1220 m.)—Ben MacDhui (4296 ft.; 1310 m.), Braeriach (4284 ft.; 1306 m.), Cairn Toul (4241 ft.; 1293 m.) and Cairn Gorm (4084 ft.; 1245 m.)—and several more just short of that figure—Cairn Lochan (3983 ft.; 1214 m.), Beinn a' Bhuird with two summits (3924 and 3860 ft.; 1200 and 1177 m.), Ben Avon (3843 ft.; 1171 m.) and Beinn Mheadhoin (3883 ft.; 1183 m.). Of the higher summits only Cairn Toul with its pyramidal top conforms to the conventional idea of a mountain; the rest, with Beinn a' Bhuird and Ben Avon and others at slightly lower elevations, are merely slight eminences in more or less extensive high-lying plateaux. These broad, flat or gently rounded summit-plateaux are characteristic of the region and present a striking contrast to the deeply dissected plateaux of west central Scotland.

The deep, narrow Lairig Ghru (summit of col 2700 ft.; 823 m.) cuts right through the highest part of the massif, dividing it into a smaller western portion (including Braeriach plateau, the largest area of land over 4000 ft. in the British Isles, Cairn Toul and the magnificent An Garbh Choire, the glacier from which debouched through the Lairig) and a larger eastern portion. The extensive plateaux of the eastern part are separated by wide major and narrow subsidiary valleys, carrying torrential mountain streams. Most of the major streams run north or south with the important exception of the Upper Avon, which flows eastwards. Several of the valleys terminate in great corries backed by precipitous crags which form a main feature of the area. Set in this background, with austerity as its primary feature, are several high-lying mountain lochs, the largest being Loch Einich (at 1650 ft.; 503 m.), Loch Avon (2377 ft.; 725 m.) and Loch Etchachan (3073 ft.; 937 m.). The small Loch Buidhe is the highest at nearly 3700 ft. (1128 m.)

* *The Scottish Mountaineering Club Guide* (1928), by H. Alexander, contains much useful information. See also the relevant *Geological Memoirs* (Hinxman, 1896; Hinxman & Anderson, 1915; Barrow & Cunningham Craig, 1912; Barrow, Hinxman & Cunningham Craig, 1913).

The corries were the feeding grounds of high-lying glaciers which deposited morainic material in their bottoms and in the valleys leading from them; elsewhere the higher ground is formed of frost-shattered granite. Boulder clay does not form a general cover except at lower elevations, although a small area of moraine occurs just north of Loch nan Cnapan at approximately 2800 ft. The even disintegration of the homogeneous granite and the effect of glaciation at the lower levels have resulted in generally smooth and well-rounded summits and spurs.
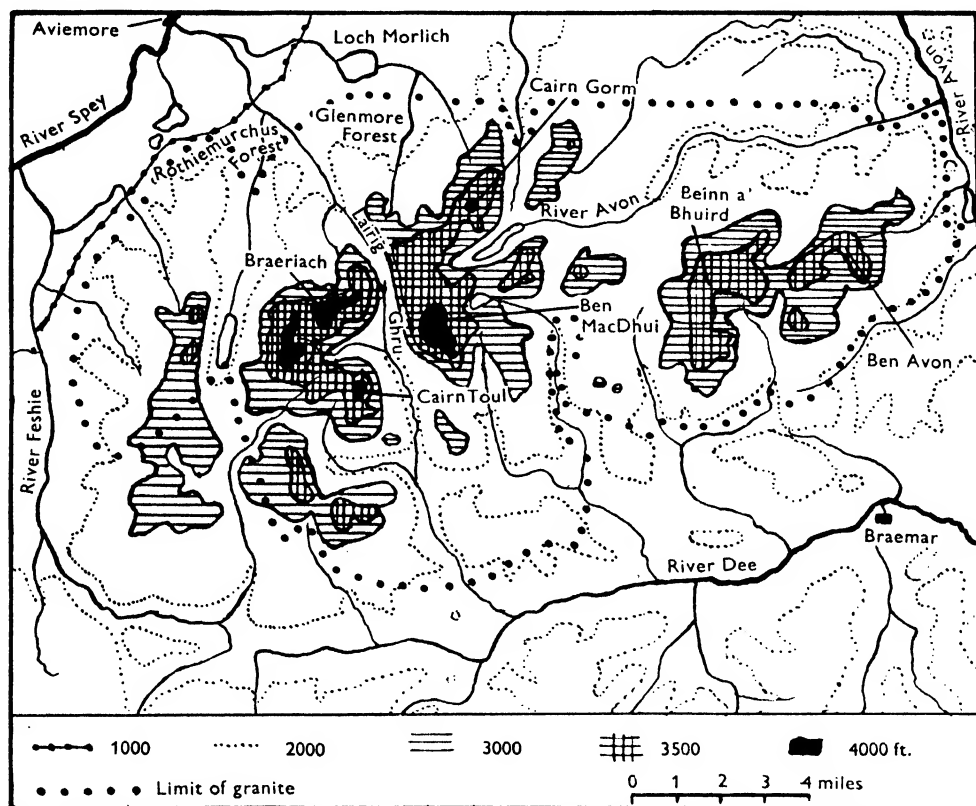
Fig. 1. Sketch-map of the Cairngorms showing the principal contours and the granite core.

Although extensive areas of deep peat are found on ill-drained flat plateaux up to approximately 2000 ft., at higher elevations deep peat is not extensive; the highest areas marked on the geological map are a small area about half a mile (0·8 km.) west of the 3860 ft. summit of Beinn a' Bhuird at approximately 2800 ft. (854 m.) to 3150 ft. (960 m.), and a larger area at Moine Mhor at about 2950 ft. (899 m.) to 3100 ft. (945 m.); both these are much eroded. Thin peat and peaty raw humus is widespread up to about 2500 ft. (762 m.), and below this altitude forms the usual covering of gently sloping or level ground which is stable and sufficiently sheltered.

Climate

There are no meteorological data from the Cairngorms themselves, so that the excellent general account by W. G. Smith (1911) of the climate at the higher elevations may be accepted, with the reminder that the application of the data obtained from Ben Nevis

needs some qualification in the light of the much greater extent of high ground in the Cairngorms in a region where the climate is much less oceanic, with a lower rainfall differently distributed throughout the year and with greater extremes of temperature. In the absence of data for temperature, cloudiness, rainfall, etc., nothing useful can be added to Smith's account, but something more about the effects of wind and the duration of snow-cover is desirable.

Wind. Although there are no records of wind velocity at the higher elevations, evidence of the erosive action of the wind is everywhere abundant. The prevailing winds are westerly, and all exposed places with a westerly aspect are swept by winds, sometimes of such violence that a man cannot stand upright; pebbles ¾ in. diameter are moved along by high winds. Not only is the surface soil swept of all its finer particles leaving behind a stony and gravelly waste, but the plants themselves are directly affected. There may also be areas of high exposure on eastern slopes, especially where westerly winds passing over a ridge top or through a gap are deflected downwards and strike a projecting brow on the eastern slope.

With elevation the effect of the wind increases. At 2000 ft. the vegetation generally forms a continuous cover, and *Calluna* grows upright and spreads centrifugally. With increasing altitude the form and height of the plants change; *Calluna* in exposed places forms a continuous windclipt mat 2 in. (5 cm.) high, the individual plants spreading more or less uniformly outwards; on very exposed but stable ground (e.g. the flat summit-plateau of Craig Derry (*c.* 2800 ft.)) the *Calluna* so hugs the ground as to form a thin carpet less than half an inch (*c.* 1 cm.) thick. In the most exposed places, usually on slopes with unstable soil, *Calluna* forms a discontinuous cover with straggling unilateral growth in a downwind direction. In exposed places above the *Calluna* belt the proportion of bare soil increases until on the exposed summit-plateaux there are few scattered plants, mainly of cushion or tufted form, set in a barren gravelly or stony waste. By implication any natural feature, be it a depression in the ground, a projecting boulder, a gentle slope with a non-westerly aspect, or even a plant provides shelter to some degree and over some more or less restricted area.

Snowfall. Similarly with snowfall: the amount increases with altitude as also its duration, and the contrast between places swept bare of snow and those where it accumulates is accentuated with altitude.

There are no exact records of snowfall, its amount and duration. The hills may be temporarily snowcapped in September, but in general it may be said that snow lies from October to May or June, although the length of the snow-free period varies much from year to year. But the period during which snow is absent cannot be equated with the period during which plant leaves can survive and function, for even before snow covers the ground frosts of such intensity may occur as to kill the photosynthetic organs at least of the vascular plants. Seton Gordon (1943) records such a lethal frost on 25 September 1942 which had killed unformed flower heads and Dr M. Ingram, on a visit to Cairn Gorm and Cairn Lochan on 4 October of the same year, found that the leaves of the vascular plants were dead although snow did not fall till about 15 October.

The distribution and amount of the snow are also of great importance, for the snow is blown away from the exposed to accumulate in the more sheltered places, the depths and the areas of accumulation depending on the degree and extent of the shelter provided. Even the smallest sheltering features, like boulders and tufts of *Juncus trifidus*, provide

nidi for the accumulation of snow in small amount. As the prevailing winds are westerly and strong the eastern slopes are markedly the more sheltered; on them snow may accumulate to some depth over considerable areas forming snowfields, while in the deep pockets of corries and in ravines around the headwaters of streams, snow may accumulate to very considerable depths and lie for varying periods—often, indeed, throughout the year in 'permanent' snowbeds.

The most famous of these 'permanent' snow-beds lies in the very large deep corrie of An Garbh Choire lying between Braeriach and Cairn Toul. It was formerly regarded as permanent, but McCoss (1934) reports that all snow-beds in the Cairngorms (including that in An Garbh Choire) disappeared in September 1933, adding that 'this is the first occasion in my experience that such a thing has happened'. Seton Gordon (1943) further reports that in 1942 the snow-bed in An Garbh Choire was so far reduced that ground completely devoid of plants of any kind was uncovered. The snow-bed in Margaret's Coffin (to be described in a later communication in greater detail) had almost disappeared in November 1914 (Seton Gordon), completely so in 1933, and again in 1942 on the occasion of Dr Ingram's visit, when he noted that the whole bed was covered by mosses and liverworts.

These records of the recent disappearance of snow from beds where it was held to be permanent are of considerable interest and importance, for there are various traditions and practices in the Highlands, and writings pertaining thereto, which suggest that snow in the Cairngorms was formerly both more abundant during the summer and more persistent. Alexander (1928) writes: 'John Taylor the King's Water Poet who visited Deeside early in the 17th. century and wrote the Pennyless Pilgrimage (1618) describes how he "saw Mount Benawne (Ben Avon) with a furred mist upon his snowie head instead of a night cap: for you must understand that the oldest man alive never saw but the snow on the top of divers of these hills, both in summer as well as in winter".' Pennant (1771) writes of 'naked summits of a surprising height..., many of them topped with perpetual snow'. Again, with reference to the snow-bed in Margaret's Coffin, Alexander says: 'the snowbed, though in some summers very diminished is said never to disappear, and tradition has it that if ever it does vanish, the Grants will lose the Seafield Estates.' This is a specific variant of a widespread tradition in the Highlands that certain lands were held on the condition of supplying a bucket of snow when required.

It may be that these reports are travellers' exaggerations inspired by the local inhabitants in the hope of gain. But whether that is so or not, these observations fall into line with the general pattern of climatic change formulated by Swedish glaciologists (Ahlmann, 1946), who conclude that 1745 saw the last Arctic maximum; they are supported by G. Manley (1946), whose inquiry into the temperature change since 1750 over this country shows a general though fluctuating rise in the mean of successive decades to a maximum in 1931–40. Their significance in the interpretation of the vegetation of the summit-plateau will be dealt with in a later part.

Soil

The granite rock weathers by vertical and horizontal cleavage planes to form boulders of varying size. The relatively rapid accumulation of these (as below corrie crags), their instability on steep slopes or movement on gentler slopes in the plastic medium created at the time of the melting of the snow, all these delay soil formation. Torrential rain and

19-2

the periodic eruption of gushing streams spread fans of sandy gravel over the former surface; and in general the widespread erosion by wind and water tends to maintain the soils in an early stage of development, especially at the higher elevations.

Where, however, the frost-shattered debris lies in place, the granite boulders weather to form 'rotten rock', disintegrating into rounded rough-edged pebbles. Finer particles in the form of glacial flour are left behind by the melting snow, but this is blown or washed away, and in exposed places only the coarse detritus is left to form the infilling between projecting subangular or rounded boulders. In less exposed places with a continuous cover of vegetation a layer of mor accumulates to varying depth and soil development proceeds to a podsol profile. It is important to note, however, that even on exposed summits and in snow-beds where there is at present no humus accumulation a podsol profile is met with. It is not known at what period and under what vegetational cover this profile was formed; it may well be a relic from a period when the climate was milder and the altitudinal limits of the vegetational belts were higher than they now are.

The chief physical characteristics of the soil are its coarseness, excessive permeability, and its inability to retain much water. Chemically (if we apply the results obtained from analysis of a soil near Aberdeen, largely composed of granitic material) the particles contain considerable quantities of lime, potash and magnesia, but they have not undergone profound chemical weathering and show only superficial chemical alteration (Hendrick & Ogg, 1916). The content in replaceable bases is low and in agreement with results for acid soils in general (Hendrick & Newlands, 1926). These data were obtained from an arable soil, however, and the general coarseness of the Cairngorm soils and the low total superficial area of the soil particles would mean a much lower content in available nutrients per unit volume. The mean pH value of a large number of samples of the surface soil is in fact only 4·0.

Only under snow-beds does one find any quantity of fine soil, which has been blown thither and accumulated on the snow. On its melting a thin layer of fine mud is deposited, much of which is removed by the melt water as the edge of the diminishing snow-patch recedes. On more level ground and in shallow depressions this mud accumulates, and often shows solifluxion terraces.

The biotic factor

Only at the highest elevations in the country have we examples of vegetation almost unaffected directly or indirectly by man. At present the Cairngorms are utilized as deer forest, and the natural state is disturbed only in so far as the herds of deer maintained may be larger than the natural vegetation can support unaided. Indirectly there must be some effect on the population of wild animals by the shooting of eagles and other carnivorous birds and mammals and by the taking of eggs of rare birds. There is little sheep grazing and no burning of heather at the higher altitudes. Formerly, however, the lower lying glens supported a scattered farming population, and cattle and sheep were pastured during the summer in suitable places (Mrs Smith, 1911). The Lairig Ghru and the Lairig an Laoigh were famous highways for the driving of cattle to southern markets. Despite these activities there is no current evidence that man has had anything but a negligible influence compared with that of climate and soil.

It is possible, however, and, indeed, likely that the altitudinal limit of tree growth has been depressed by direct and indirect human activity; direct by the extensive felling of

timber more than a century ago, and indirect by the grazing of deer which checks the establishment of self-sown pine and other trees. Further information on this topic is given in the section dealing with the upper limit of pinewood (*vide* p. 295).

Flora

'The higher Cairngorms cannot be called rich in the more strictly Alpine plants especially if compared with the Lochnagar group' (Trail, 1895) in which Glen Callater, Canlochan and Glen Clova are included. And Smith (1911) notes the relative poverty of the granitic Cairngorms compared with these places and with Breadalbane in Perthshire. This relative floristic poverty is due to the absence of any large area of base-rich rocks, but the small areas of limestone which do occur and larger areas of rocks less acid than granite (e.g. diorite) support a richer flora than that of the granite.

Adjoining the granite core there are areas of limestone. To the north-east there is a narrow belt deeply trenched by the Builg and the Avon rivers; the valley sides bear floristically rich calcicolous pasture, abundant juniper and hazel scrub and birchwood. At 1200–1700 ft. *Polystichum lonchitis,** *Saxifraga aizoides,* *S. hypnoides* (agg.) and *Carex capillaris* are abundant, and many bryophytes which are absent from the granite region occur, e.g. *Amblyodon dealbatus,* *Pottia latifolia,* *Swartzia montana* (rare on granite), *S. inclinata* and *Lophozia muelleri.*

The most famous of the floristically rich patches is Creag an Dail Bheag, of which Trail says, 'at 2400–2800 ft. on a rather bare slope with broken rocks, there is an exceptionally rich Alpine flora, richer than on any similar area of the higher Cairngorms'. The geological map shows a small patch of limestone. Wherever, in fact, limestone is marked on the map, species are present which indicate a base-rich soil. Reciprocal aid may be suggested to the geologist, for at the western entrance to the Pass of Ryvoan there is an assemblage of basiphilous species (and a disused limekiln) which suggests limestone, although there is no record of it on the geological map. The species in this area include *Asperula odorata,* *Botrychium lunaria,* *Fragaria vesca,* *Linum catharticum,* *Paris quadrifolia,* *Plagiochila asplenioides* and *Sanicula europaea.* All these are essentially rare in the region. The pH of a surface-soil sample is 6·2. It is interesting that juniper is also common here, although apart from the limestone areas near Braemar and the pinewoods in Glenmore and Rothiemurchus juniper is by no means common in the Cairngorms.

The summit of Creag Coinnich (1764 ft.; 538 m.), the little conical hill just to the east of Braemar, is another area where limestone is not marked on the geological map, although ít is so nearby. On different parts of the irregular terrain of the summit there are a grazed pasture, a· very open community with 95% of the ground bare, and a floristically rich patch less than 100 sq.ft. in area. All three communities indicate a base-rich soil, the last including the following species: *Helictotrichon pratense,* *Briza media,* *Carex pulicaris,* *Galium boreale,* *Helianthemum nummularium,* *Linum catharticum,* *Pimpinella saxifraga,* *Potentilla crantzii,* *Rubus saxatilis,* *Saxifraga aizoides,* *Thymus serpyllum* and the moss *Ditrichum flexicaule.* The rock effervesces with acid, and the pH of a surface soil sample is 6·7.

The occurrence at relatively low elevations of what, for the size of the areas involved, are communities rich in species strongly supports the view that the overriding factor in

* For the vascular plants the nomenclature followed is the *Check-list of British Vascular Plants* (1946); for mosses, H. N. Dixon's *The Student's Handbook of British Mosses,* and for liverworts, S. M. Macvicar's *The Student's Handbook of British Hepatics.*

determining the floristic poverty of the higher Cairngorms is the absence of suitable base-rich rocks. Yet within the granite area itself the presence of certain species seems to indicate a local concentration of minerals in excess of the average. Thus Dickie (1860) gives Ben Avon, Ben a' Bhuird and Ben MacDhui as localities for *Dryas octopetala* and Ben MacDhui for *Saxifraga oppositifolia*, species which are commonly associated with base-rich rocks, certainly with rocks of higher base content than the normal granite of the Cairngorms. That there are such patches with a higher base content than the average is shown by a value of pH 5·3 for a soil from a crevice on a steep rocky slope between Loch Einich and Braeriach plateau. It supported *Veronica alpina*. Granite, however, is not necessarily homogeneous, and a higher felspar content or contamination with neighbouring rock may account for local variation. Further data are required.

Because base-rich soil is local and of small extent basiphiles contribute little to the vegetation as a whole. The chief dominants are *Calluna vulgaris*, *Arctostaphylos uva-ursi*, *Vaccinium myrtillus*, *V. vitis-idaea*, *V. uliginosum*, *Empetrum hermaphroditum*, *Loiseleuria procumbens*, *Juncus trifidus*, *Carex bigelowii*, *Nardus stricta*, *Deschampsia caespitosa*, *D. flexuosa*, *Salix herbacea*, *Rhacomitrium lanuginosum*—all plants tolerant of acid soil. But the monotony arising from floristic poverty is relieved by the presence of the acid-tolerant and rare arctic species of corrie, snow-patch and summit plateau, and is largely offset by the varying form of the dominants and the changing pattern, both the small-scale pattern within the community and the larger involving different communities.

THE AREA INVESTIGATED

The area intensively investigated is the high-level plateau of Creag an Leth Choin, Cairn Lochan, Cairn Gorm and Cnap Coire na Spreidhe and the series of spurs and broad-bottomed valleys running north-north-west from this plateau towards Loch Morlich (Figs. 2, 3). The high-level plateaux of Ben MacDhui and Braeriach were also examined but not in detail.

In general, the spurs have rounded contours, Sron an Aonaich, up which the path leads to Cairn Gorm, being typical, but Fiacaill a' Choire Chais and the upper part of Fiacaill a' Coire an t'Sneachda are exceptional in forming narrow ridges with large boulders. The valleys are in places overdeepened with their streams running in narrow V-shaped trenches.

At the heads of the four main valleys lie the four corries: Coire an Lochain, Coire an t'Sneachda, Coire Cas, Coire na Ciste. The first two are much alike; the small lochs lying at just over 3000 ft. are overlooked by precipitous crags rising 600–900 ft. above them; the gullies and ledges, dry or with trickling or running water, provide specialized habitats, whose soil is much less earthy and less cohesive than that found in similar situations on Ben Lawers. Coire Cas is dry, gravelly, steep but not precipitous, while the head of Coire na Ciste is a shallow depression lying at about 3500 ft., at the upper part of which issues a series of strong springs. All these face north.

In these four corries snow lies late—until the end of June in 1939. Facing east and protected by the ridge running north-north-east from Cairn Gorm and about ½ mile (0·8 km.) north-east from the summit lies the deepish gully known as Margaret's Coffin, already alluded to, where the snow-bed is subpermanent.

The summit of Cairn Gorm is broadly dome-shaped with about $\frac{1}{16}$ sq. mile (16 hectares) lying above 4000 ft. A much greater expanse of plateau, at just under 4000 ft., extends southwards from Cairn Lochan. West of this plateau the ground slopes fairly steeply, but
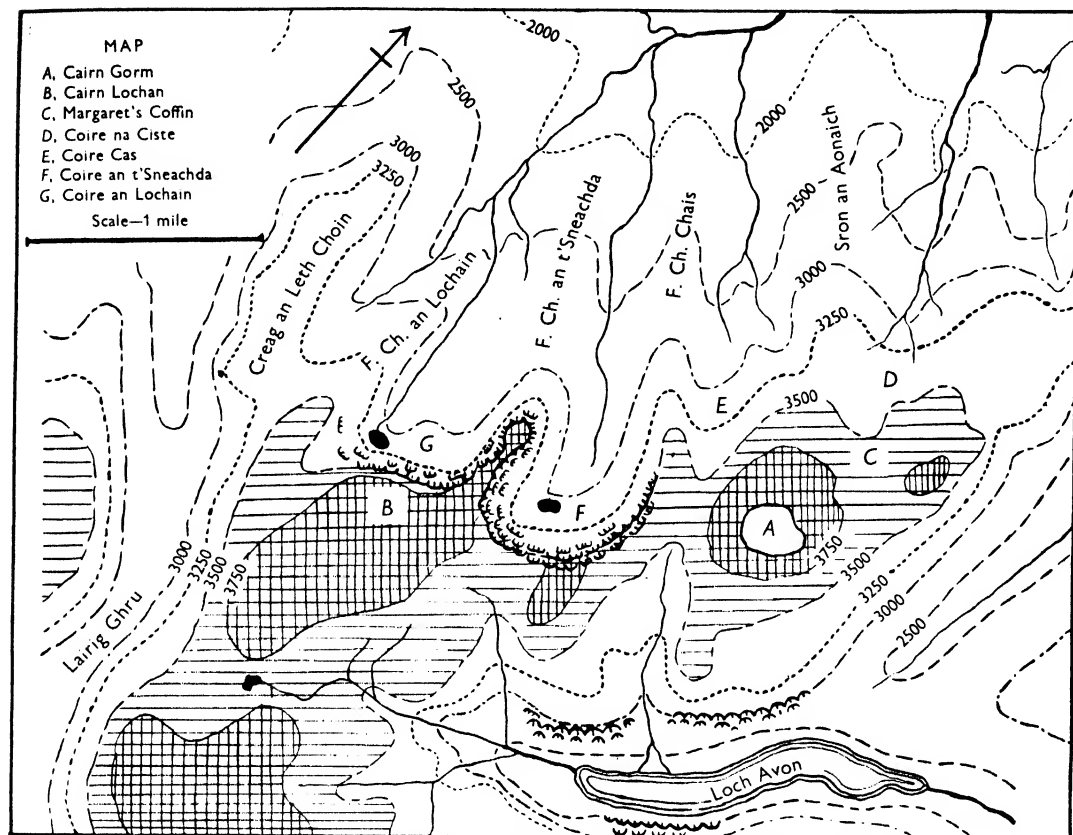
Fig. 2. Map of the main area of investigation showing the chief physical features.
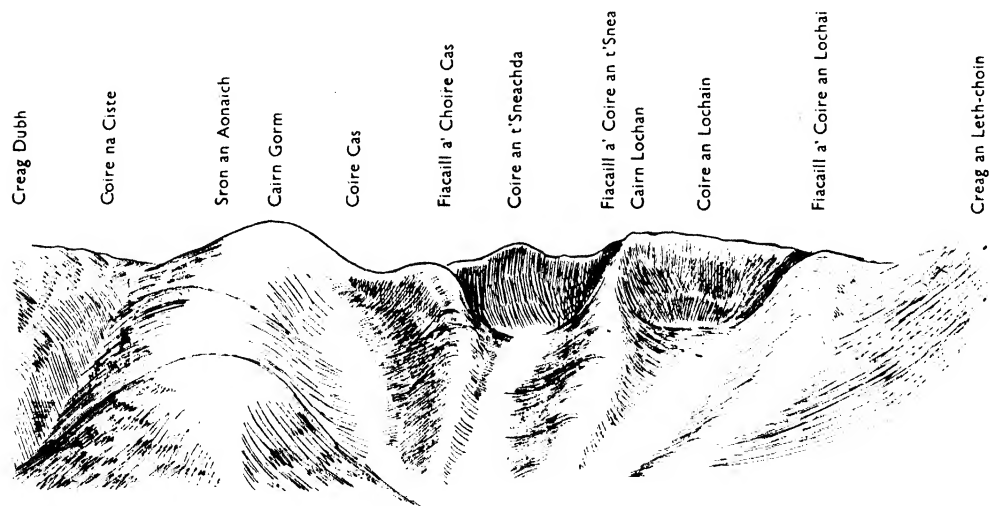

Fig. 3. Sketch of the area looking up the valleys and south towards Cairn Gorm, the corries and the plateau.

to the east much more gently. The two slopes have strikingly different microclimates; the western is wind-swept, the eastern is more sheltered and snow accumulates on it to form a snowfield.

The terraces

While the broad pattern of the vegetation is related to altitude, exposure and duration of snow, the details of the floristic and physiognomic mosaic within any one altitudinal zone can be understood only if account is taken of the minor variations in microclimatic and soil factors associated with the minor topographic variations found on the terraces. For much of the surface of the area investigated is terraced from about 2000 ft. upwards. The feature is so striking and so fundamental to an understanding of the distribution of plant communities and their physiognomic variation, that the omission of any reference to them in the *Memoirs of the Geological Survey* dealing with the region renders some account of them necessary (Pl. 22, photos 1, 2).

Although the phenomenon of terracing is widespread in the Cairngorms, terraces are far from being uniformly distributed. By and large they are more abundant on these northern slopes than elsewhere. Usually they are arranged topographically side by side and one above the other, giving the hillside the appearance of an irregular flight of steps. In such cases the whole hillside is terraced, but there are slopes where occasional terraces only break the uniformity of a smooth slope.

Terraces are found on slopes of varying steepness and aspect, in screes of massive boulders, in moraine of the valley bottom and margin, in the frost-shattered rubble covering the bulk of the higher ground and in the muds of some snow-beds. Besides differing in the material of which they are composed, terraces vary much in size and shape as well as in the details of their structure, in the slope and composition of the platform, and in the height, slope, curvature and composition of the retaining bank. But essentially they consist of a platform with a relatively uniform slope and a retaining bank.

Terracing is referred to in *Geological Memoirs* dealing with the north-west of Scotland (Peach *et al.* 1912; Peach *et al.* 1913; Crampton *et al.* 1914), for example, the plateau debris is arranged in 'narrow subparallel terraces separated from one another by small nearly vertical scarps, often from one to three feet in height' (1912). The cause of the phenomenon is given as gravity (1914), earth creep (1912), 'soil creep aided by the movement of snow' (1913) and possibly also 'induced by freezing and thawing of water in the lower layers' (1914). In all these terraces the material appears to be debris or rubble without much infilling between the stones. It may be added that large terraces, some with banks 4 ft. high, are well developed near the summit of 'The Castles' (Caisteal Abhail) in Arran, while broad, shallow terraces occur in the summit of Great Gable, and probably elsewhere in the Lake District.

The conditions in the Cairngorms under which gravity would act most effectively would obtain during the period of snow-melting when the surface layers as a whole would form a sludge over a substratum still frost-bound. In Margaret's Coffin, on the terraced slope recently uncovered by melting snow, the pressure downhill of the brown soupy mud lying between the relatively firm surface and the frost-bound substratum would tend to produce a terrace where some barrier offers sufficient resistance to downward movement. In this case drying-out would be sufficient. The essential conditions in terracing in general appear to be a flow and a barrier or retaining bank holding it up. The barrier may be

Phot. 1. View eastwards from Sron an Aonaich at about 2500 ft. The foreground is occupied by a terrace with part of the bank on the right bearing *Vaccinium myrtillus*. Across the terrace platform from right to left is a series of zones dominated respectively and in order by *Nardus stricta*, *Empetrum nigrum* and tall *Calluna vulgaris*, and short *Calluna* with some *Loiseleuria procumbens*. The background shows terracing (light and dark shade), the extent of bare eroded ground and the strips of *Calluna*. Phot. by G. Metcalfe.
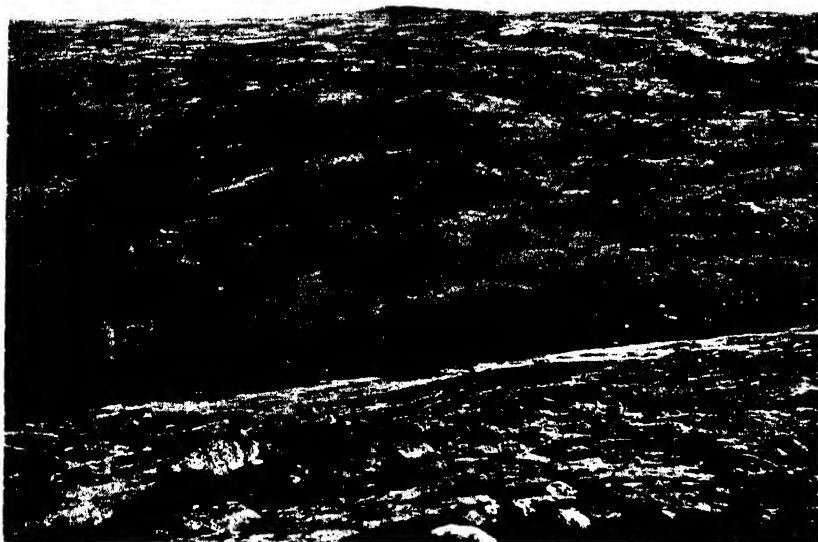
Phot. 2. North-west facing slope of Cnap Coire na Spreidhe, showing terraces at 3000–3600 ft. Phot. by N. A. Burges.

generated by the system itself, and boulders may be visualized as moving forward down-hill at each mobilization and piling up in or against the bank, whose beginnings may have been due to a local obstruction or simply the absence of the conditions necessary for flow. In such instances the retaining bank would bear an obvious relation to the contour of the hillside. But there are terrace systems where the retaining banks run athwart the contour; and the assumption of the pre-existence of banks of boulders, once external to and now forming retaining banks of terraces, is justified by their separate existence and independence of the contour. No suggestion is made as to the origin of these banks of boulders.

While the primary cause of terracing is solifluxional, there are adventitious factors modifying the details of structure. These are the transport of material both within the system and to and from it by wind and water. Pits dug in the platforms of many terraces show a buried soil surface or surfaces overlaid by sandy gravelly deposits, which, it is assumed, were brought down from above by water. Examples of fresh deposits were seen. Also some retaining banks are completely buried by debris moved over the brow of the terrace (Fig. 4). On the more exposed brows, where vegetation does not form a continuous cover, erosion by wind and water with the help of vegetation itself results in the formation of a series of terraces of a minor order.

Fig. 4. Profile through a terrace in the *Empetrum-Vaccinium* zone, showing the differential effect of the habitat on the vegetation. A superficial raw humus layer is continuous throughout, but in the angle of the terrace an earlier raw humus layer has been buried by debris which shows differentiation into A_0, A_1 and A_2 soil horizons.

For our present purpose the significant fact is that the topographic variation gives rise to microclimatic and soil variation within the terrace unit. Microclimatically the brow of the terrace is the most exposed to wind, and the angle between the bank and the platform is the most sheltered; the rest of the terrace unit is transitional between the two extremes, exposure increasing both up the bank and along the platform with distance from the sheltered angle. Both the depth and duration of the snow cover will also vary, being greatest in the angle and least on the brow. The amount of the melt water will vary in the same sense. The base of the bank and the angle tend to be the dampest parts of the terrace through seepage to the surface at this point of telluric water, the amount of which varies much. Between the extremes of dry terraces in which the whole terrace including the angle is dry, and wet terraces in which flowing water issues from the angle or drips from the bank above, there are all transitions.

The ecology of the Cairngorms

But in all cases there is a gradient in wetness and in depth of the water table from the angle to the dry exposed brow. Thus the terrace unit is differentiated into a graded series of habitats, differing in their moisture relations, in exposure to wind, and in the amount and duration of the snow-cover, and the differentiation may be sufficiently great to lead to
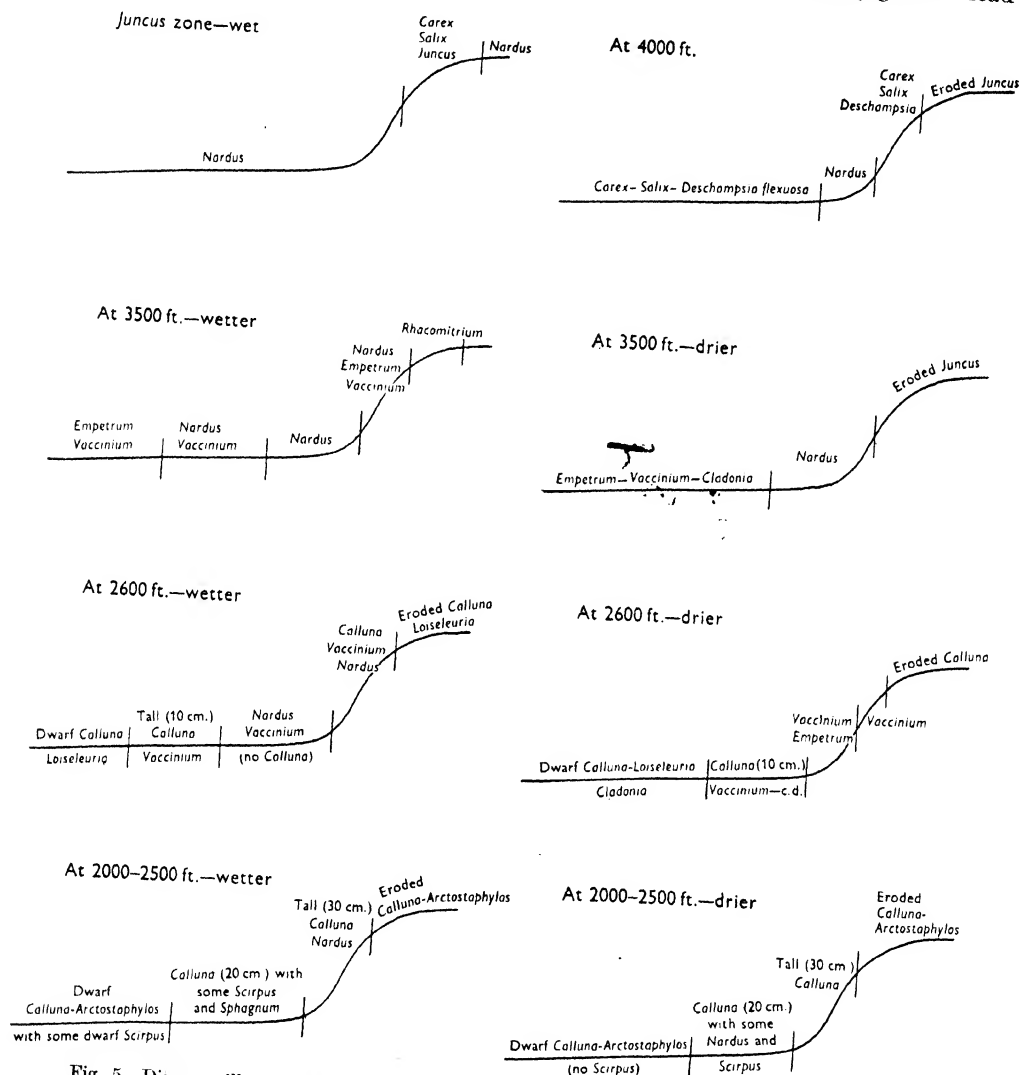

Juncus zone—wet
Carex
Salix
Juncus | Nardus
At 4000 ft.
Carex
Salix
Deschampsia | Eroded *Juncus*
Nardus
Carex- Salix- Deschampsia flexuosa | Nardus

At 3500 ft.—wetter
Rhacomitrium
Nardus
Empetrum
Vaccinium
Empetrum
Vaccinium | Nardus
Vaccinium | Nardus
At 3500 ft.—drier
Eroded *Juncus*
Nardus
Empetrum—Vaccinium—Cladonia

At 2600 ft.—wetter
Eroded Calluna
Loiseleuria
Calluna
Vaccinium
Nardus
Dwarf Calluna | Tall (10 cm.) Calluna | Nardus Vaccinium
Loiseleuria | Vaccinium | (no Calluna)
At 2600 ft.—drier
Eroded Calluna
Vaccinium | Vaccinium
Empetrum
Dwarf Calluna-Loiseleuria | Calluna (10 cm.)
Cladonia | Vaccinium—c.d.

At 2000–2500 ft.—wetter
Eroded
Tall (30 cm.) Calluna-Arctostaphylos
Calluna
Nardus
Dwarf Calluna-Arctostaphylos with some dwarf Scirpus | Calluna (20 cm.) with some Scirpus and Sphagnum
At 2000–2500 ft.—drier
Eroded Calluna-Arctostaphylos
Tall (30 cm.) Calluna
Calluna (20 cm.) with some Nardus and
Dwarf Calluna-Arctostaphylos (no Scirpus) | Scirpus

Fig. 5. Diagram illustrating the variation of the vegetation with altitude, with the 'wetness' of the terrace as a whole and with position on the terrace.

the segregation of a series of distinct plant communities on the same terrace unit, or may merely affect the frequency, vigour and habit of certain species within the community covering the whole or the greater part of the terrace (Fig. 5).

One result of this differentiation of the habitat is the interdigitation of the altitudinal zones of vegetation, outliers of contiguous zones occurring in suitable habitats of the

neighbouring one, it may be at some considerable distance from the general boundary between them. In fact, data of altitudinal limits have little meaning when divorced from the topographic complex.

ALTITUDINAL ZONATION

The upper limit of forest

In the forests above Braemar on Deeside, birch and pine are the characteristic dominants, and a cursory examination of them suggests base status of the soil as one, if not the important differentiating factor. There is a similar sharing of dominance on Speyside. But in the natural forests of Glenmore and Rothiemurchus on the northern slopes of the Cairngorms and in Glen Derry, Glen Quoich and Gleann an t'Slugain on Deeside, it is the pine which forms the upper limit of the forest.

This upper limit varies much from place to place and cannot be correlated with any obvious climatic factor such as exposure.* In fact, the upper limit in most places appears to lie well within the climate permitting tree growth. On the way from Glenmore Lodge to Cairn Gorm the last scattered outposts of the forest at about 1700 ft. (518 m.) are 30–40 ft. (9–12 m.) high, well grown and symmetrical. Pines at higher elevations (up to 2200 ft.) and more exposed places (e.g. in Upper Glen Quoich) are smaller, but their shape is not markedly affected by wind.

There is a noteworthy absence of young trees both just below and above the tree limit. Yet seed would appear to be provided in plenty if one may judge from the numerous seedlings, established in the mineral soil of the path above its emergence from the forest in Gleann an t'Slugain at about 1500 ft. A 3-year seedling has, in fact, been seen within 50 ft. of the summit of Morrone (i.e. at 2769 ft.; 844 m.); it was on the exposed western side and established in mineral soil. A more instructive pine was collected from the northern slope of Cairn Gorm at 2670 ft. (803 m.). It was 9 in. (22 cm.) high and erect. It had been grazed and had lost its leading shoot at least five times; its leaves, from $\frac{1}{2}$ to $\frac{3}{4}$ in. (1–2 cm.) in length, survived 2 years, and its approximate age was 20 years. It is impossible to assess how much of its depauperate condition was due to grazing and how much to the rigours of the climate at that altitude.

Further support to the view that the present tree limit is almost everywhere biotic and not climatic may be obtained from the occurrence of trees on rocky precipices where, because inaccessible, they have a greater chance of escape from grazing. Thus at 2325 ft. (709 m.) on the precipices of Creag an Dail Bheag birch and larch (*Larix decidua*) up to 1 ft. (30 cm.) in height have been seen. Rowan (*Sorbus aucuparia*) emerging from between boulders and 15 in. (37 cm.) high was recorded at 3200 ft. (975 m.) in Coire an t'Sneachda.

It may be added as a matter of interest that self-sown larch (*Larix decidua*) has been recorded at 2725 ft. (831 m.) on Morrone and at 2950 ft. (899 m.) on Glas Maol (Roger, 1941); in the former locality the larch is a 'rather prostrate but robust shrub', and the neighbouring flora is reported to include *Loiseleuria procumbens*, *Empetrum nigrum*, *Calluna vulgaris*, *Carex bigelowii* and *Rhacomitrium lanuginosum*; on Glas Maol (which is about 9 miles (14·5 km.) south of Braemar and not a part of the Cairngorms) the soil is

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* A climatically imposed limit is obvious from the forms of the pines at and just below the present upper limit of 2120 ft. (648 m.) on Creag Fhiaclach on the north-western fringe of the Cairngorms. Fully exposed to westerly winds, the pines are from 0·5 to 1 m. high, bushy and much branched, some with horizontal branches 4·5 m. long. The needles are from 2·0–2·5 cm. long.

micaceous schist, the larch is 10 in. (25 cm.) high and the accompanying species include *Dryas octopetala*, *Salix reticulata* and *Silene acaulis*.

Quite apart from the interesting problem of the conditions under which the pine most easily and successfully regenerates itself, the evidence points to the conclusion that the present limit of the pine is not determined by climate. What the limit imposed by climate would be in the sheltered interior valleys is unknown.

Note on the altitude of pine buried in the peat

In the series of papers by Lewis subfossil pine is stated to occur at various maximum altitudes in this country: 'forest remains are abundant on the summits in the peat of the Grampians at more than 3000 ft. above sea-level' (1906); 'Upper Forest rises to close on 3500 ft.' (1907); 'a forest of pine, hazel and birch occurring up to 3200 ft. above sea-level' (1911). No locality is mentioned. Samuelson (1910) obviously doubted the accuracy of these statements and quotes Geikie (1874) who, in turn, drew his information from Grant, who contributed an account of the parish of Kirkmichael to the *Statistical Account of Scotland* (Sinclair, 1794). Grant says: 'In Glenavon, of this parish, are mosses, near 3000 ft. above the level of the sea, full of the fir root.' The record requires confirmation, for no peat at that level is marked on the Geological Survey Map. There is, however, an abundance of peat at 2000 to *c.* 2400 ft., and Lewis himself reproduces a photograph of buried trees at 2200 ft. in Coire Riabhach some 7 miles east of Strath Avon. We have ourselves recorded an isolated pine at 2400 ft. from thin peat in our area. In the much-eroded peat at Moine Mhor (2900–3100 ft.), and in the flat plateau (2800 ft.) north of Craig Derry, there are certainly no obvious tree remains.

On an appeal to the Assistant Director of the Geological Survey in Scotland the following facts were kindly supplied by Dr J. B. Simpson. In Upper Deeside tree roots or stumps were recorded up to 2000 ft. in Geldie Burn, Glen Ey and Bynack Burn; there is no record of tree remains in peat above this level. On the Monadliaths, between Spey and Findhorn, the highest record for pine is 2150 ft. and for birch 2332 ft. Dr Simpson adds: 'In this area thick peat mosses extend unbroken between 1000 and 3000 ft., and it seems to me a very significant fact that three different surveyors frequently record pine stumps up to 2000 ft., but very rarely above this level in those mosses. At the higher levels they often record the peat as haggy and wasted and obviously would have noted stumps if these were present' (*in litt.* 1946).

Zonation above the forest

Above the forest the altitudinal limits of the zones of vegetation are probably determined by physical factors alone, of which the most important are altitude (temperature), exposure to the prevailing winds and duration of snow. Since exposure and duration of snow are intimately related, these two factors may be taken together as one variable and used with altitude as the other variable to form a simple diagram depicting the result of their interplay on the vegetation (Fig. 6). This is an oversimplification of the actual situation, but forms a suitable general introduction to the more detailed accounts to follow.

The *Calluna* zone forms a continuous belt round the middle slopes. Above it the vegetational pattern is a close reflexion of the physiographic pattern in which exposure and snow-cover become increasingly important relative to altitude. The communities of this vegetational pattern fall naturally into three groups: the *Empetrum-Vaccinium* zone, the *Juncus trifidus* zone and snow-patch vegetation.

These zones, communities and community complexes are climatically limited. There are other communities found at various altitudes in which the master factor is edaphic; in particular at higher altitudes there are the communities dominated by *Deschampsia caespitosa* near the headwaters of springs, and those on wet ground over a wide range of altitude dominated by *Nardus stricta*. Between these *Nardus* communities and those irrigated by melt water from snow-patches there is no sharp dividing line. Also on overdrained bouldery substrata communities dominated by *Rhacomitrium lanuginosum* are found in the *Calluna, Empetrum-Vaccinium* and in the *Juncus* zones.
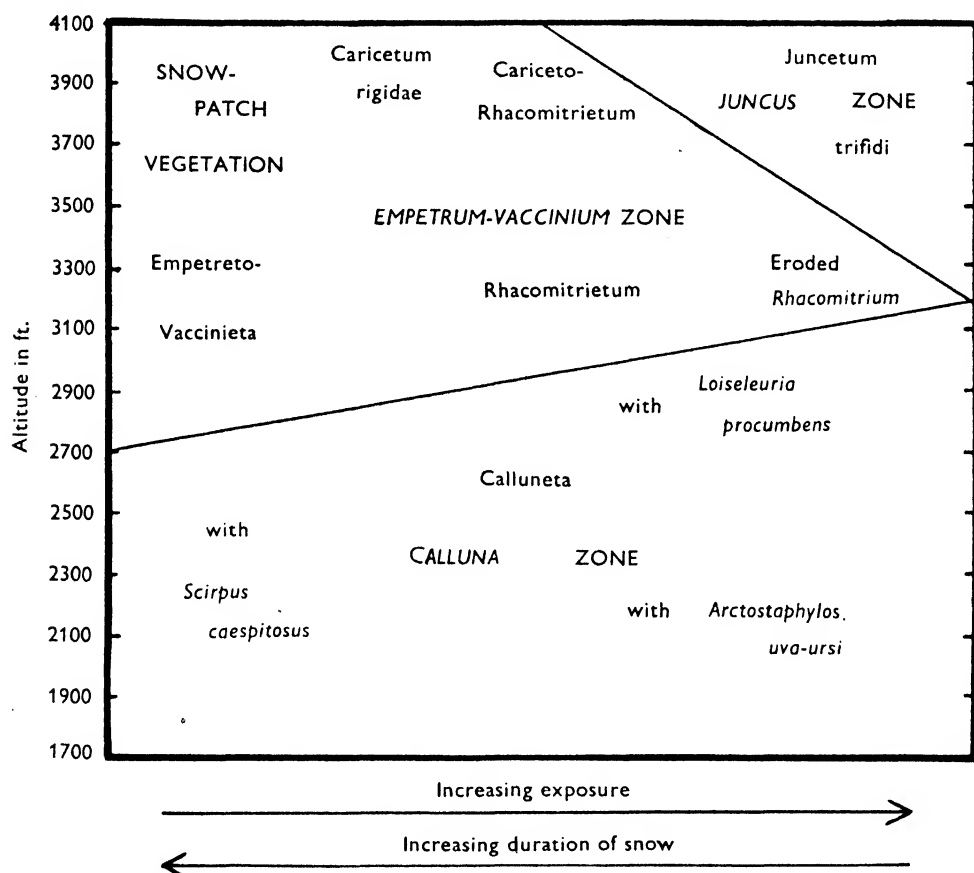
Fig. 6. Diagrammatic representation of the interaction of altitude, exposure and snow-cover on the distribution of the chief plant communities.

Calluna *zone*. The transition from pine forest to Callunetum is abrupt without any scrub of juniper, willow or birch. The absence of a low scrub above the forest upper limit is, as far as our experience goes, the normal state in the Scottish Highlands. In this respect Scandinavian and Swiss vegetation is strikingly different. But how far the absence of such a scrub inheres in natural British vegetation and how far it may be due to biotic and human action it is impossible to decide in the absence of further observation and experiment. Certainly the existence in some parts of the Highlands of a low willow scrub on crags inaccessible to animals suggests at least that the biotic factor may be responsible.

On well-drained soils and up to quite high altitudes in the Cairngorms and generally on the mountains in north-eastern Scotland the widespread dominance of *Calluna* is a characteristic feature. At comparable altitudes in central and west central Scotland grassland of fescue-bent and variants with *Nardus* and *Juncus squarrosus* determine the general aspect. Within the Cairngorm area such grassland is rare, and its occurrence is usually associated with past cultivation or with steep slopes and with rocks less acid than granite. Just south of the Cairngorms on the micaceous schist of Glas Maol and farther south near the Spital of Glen Shee fescue-bent communities dominate the landscape.

From the edge of the pinewood to about 2800 ft. (854 m.) *Calluna vulgaris* is the dominant species, responding in its height, density and habit to the increasing rigour of the climate with increasing altitude. Isolated plants of a straggling, one-sided growth are found in exposed and eroded situations up to an altitude of 3400 ft. (1036 m.). The highest altitude at which *Calluna* has been seen is 3595 ft. (1095 m.) on the western slopes of Ben
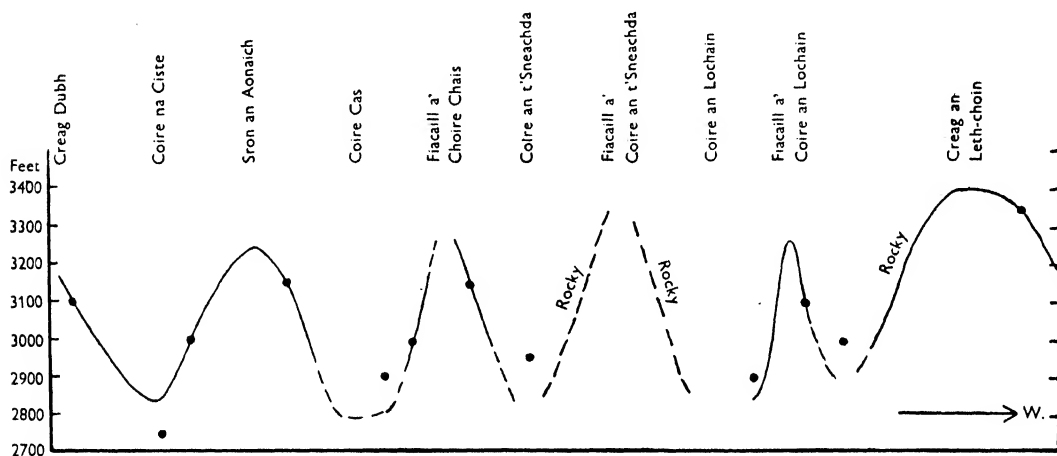
Fig. 7. Scheme showing the relation between the upper altitudinal limits of *Calluna* and exposure. The data indicate that unless the conditions are exceptional *Calluna* ascends higher on exposed slopes and is excluded from sheltered places where snow lies longer.

a' Bhuird. The plant was isolated, about 4 in. (10 cm.) high but young, healthy and vigorous (September 1947). In sheltered valleys, however, the maximum altitude is much less. The upper limit of Callunetum similarly varies. The records show that in general Callunetum ascends highest on the exposed slopes of spurs and has a low upper limit in the valleys, particularly in narrow valleys, both in their bottoms and on the sheltered east-facing slopes. To this general statement the low maximum altitude on Fiacaill a' Coire an t'Sneachda is an exception, whose explanation may be sought in the rocky terrain of the ridge which is unsuitable for the establishment of *Calluna* (p. 301).

Callunetum ascends on exposed west-facing slopes to a maximum altitude of 3150 ft. A simple explanation of its exclusion from the higher altitudes in valleys, especially in narrow valleys, is to be found in the inability of the species to endure long-persisting snow which accumulates in such sheltered places (Fig. 7). Fig. 8 shows diagrammatically the distribution of Callunetum and Empetro-Vaccinietum (and Nardetum) in the deep narrow valley below Coire na Ciste and the possibility of relating such a distribution to the duration of snow-cover. Even deep in the *Calluna* zone, *Calluna* is absent from the

rocky banks of many terraces; and at as low an altitude as 2000 ft. in a pocket about 15 ft. deep and 20 ft. across, *Calluna* is a rare and small plant in a vegetation with *Vaccinium myrtillus* and *V. uliginosum* the most abundant species. The accumulation and persistence of snow afford an adequate explanation of the differentiation in and about the pocket and a partial explanation of the exclusion of *Calluna* from the rocky banks (*vide* below).

A primary distinction is made between a dry and a moister, peaty Callunetum. The latter is found on more sheltered and gentler slopes; with *Scirpus caespitosus* as the common associate of the *Calluna*, it forms a community which is widespread on British moorlands from which specifically alpine species other than *Rubus chamaemorus* are absent.
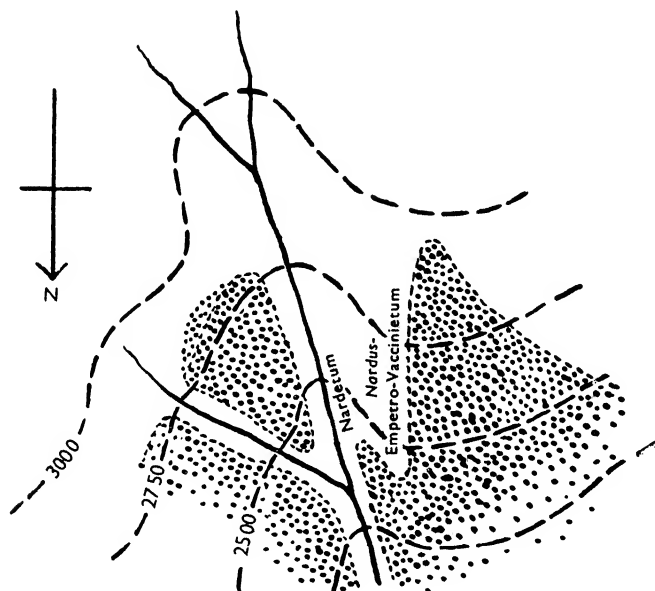
Fig. 8. Detail of the lower part of Coire na Ciste showing distribution of the Callunetum (stippled) in relation to contours and exposure to westerly winds.

The drier Callunetum is characteristic of exposed ground. It is subdivided into an upper Callunetum with *Loiseleuria procumbens* and a lower with *Arctostaphylos uva-ursi*, differentiating species whose lower and upper limits respectively fall within the *Calluna* belt.

Arctostaphylos has a general upper limit at about 2600 ft. (792 m.) with a maximum at 3000 ft. (914 m.). Its abundance is related to the behaviour of its chief competitor *Calluna*. The relations between these two species under different sets of conditions have been worked out in detail by Dr G. Metcalfe, who shows that *Arctostaphylos* by vegetative spread may colonize bare ground and be ousted later by the lateral spread of *Calluna*. In the most exposed places where *Calluna* is patchy *Arctostaphylos* may occupy much of the ground; in sheltered places at the higher elevations *Arctostaphylos* is absent from closed Callunetum, but at lower elevations it maintains itself.

Loiseleuria procumbens descends lower on the ridges than in the valleys, with a general lower limit at about 2500 ft. and a minimum at 2000–2200 ft., where the competitive power of *Calluna* is reduced by exposure. Its general upper limit in this area is 3000–3200 ft., but it is found up to 3700 ft. in eroded situations where shelter is provided by

cushions of other plants, e.g. *Rhacomitrium*. Outside the area, as, for example, on the summit plateau of Lochnagar (Alexander, 1928) *Loiseleuria* is common, as it is on an exposed east-facing slope on Ben a' Bhuird at about 3000 ft. along with much *Calluna* and *Empetrum hermaphroditum*.

The differentiating factor which allows *Vaccinium vitis-idaea* to ascend higher in the valleys to a maximum of 3000 ft. than on the ridges where the maximum is much less at 2400 ft. would appear to be the shelter-snow-cover complex. (Compare *V. myrtillus*, whose dominance is related to the same complex.)

Empetrum-Vaccinium *zone*. On the most exposed slopes the *Calluna* zone merges directly into the *Juncus* zone above it through an ecotone of mixed *Calluna* and *Juncus trifidus*. Elsewhere snow-cover depresses the upper limit of the *Calluna* zone; above it lies the *Empetrum-Vaccinium* zone. This zone reaches the summit plateau on suitable terrain, but from the most exposed places it is absent, as also from the most sheltered where snow lies long in subpermanent beds.

The most important species are *Empetrum hermaphroditum*, *Vaccinium myrtillus*, *V. uliginosum* and *Rhacomitrium lanuginosum*, forming two well-marked communities, the Empetreto-Vaccinietum and the Rhacomitrietum. The habitat preferences of these two are indicated in the diagram; the *Rhacomitrium* is found in well-drained places of medium exposure and little snow, the Empetreto-Vaccinietum on well-drained soil where the shelter is greater and the snow lies longer.

These conclusions, based on the relatively inextensive examples in the area closely studied, are supported by the Rhacomitrietum crowning the summit of the long ridge just west of Loch Einich at an altitude of approximately 3250–3500 ft. At a similar altitude, the Empetreto-Vaccinietum occupies the large, relatively sheltered, horseshoe-shaped shallow basin occupying the eastern edge of the Ben Avon plateau. In the plateau above, at c. 3600 ft., *Rhacomitrium lanuginosum* and *Juncus trifidus* are the most abundant species. Additional evidence for this habitat relation comes from the juxtaposition of these two communities on certain terraces, where the Rhacomitrietum is always nearer to or on the exposed brow of the terrace, that is, in a situation more exposed and drier, where there is less snow which persists for a shorter time.

Between these two communities and their neighbours, gradations form complexes showing the changing relation between the important species with change in the habitat. Ecotones of *Calluna-Empetrum*, *Calluna-Rhacomitrium* and the *Rhacomitrium-Juncus* mentioned above are examples. They may form narrow belts in one area, or broad in another; their status is best elucidated by reference to the behaviour of the dominant or most abundant species.

The conditions under which *Rhacomitrium lanuginosum* dominates have been indicated above, but the species is widespread, occurring from sea-level to the mountain tops and in sheltered as well as exposed places above 2000 ft. It is also the most important pioneer and ultimately the characteristic dominant of rough overdrained terrain of medium-sized boulders without soil infilling between them.

Vaccinium myrtillus also ranges from sea-level to the tops of the highest mountains. In the Cairn Gorm area its vigour and density vary much. It is not, as its dominance in the 'Vaccinium edge' community in the southern Pennines might lead one to expect, a plant of the most exposed places. For in the *Juncus* zone and in the *Juncus-Calluna* ecotone it is an infrequent and dwarf plant. This inability to endure dry exposed conditions less well

than *Calluna* is also clear from the behaviour of these two species on certain terraces. In the angle of the terrace and on the upper part of the platform *Vaccinium myrtillus* grows well along with vigorous *Calluna*; on the exposed brow where windclipt *Calluna* is abundant, *Vaccinium* is virtually absent.

On the other hand, *V. myrtillus* flourishes in screes from which *Calluna* is practically absent. It occurs almost alone on the rocky banks of certain terraces which are essentially miniature screes. And on screes at all altitudes *Vaccinium* is a vigorous and successful pioneer (Leach, 1930). When, however, the interstices between the boulders become filled with debris *Calluna* becomes dominant. We may thus conclude that while the vegetative spread and tolerance of shade allow *Vaccinium myrtillus* to persist in such rocky substrata the establishment by seed of the intolerant *Calluna* is prevented. This would account for its absence as a dominant from the exposed rocky arête of Coire an t'Sneachda.

The recognition of an *Empetrum-Vaccinium* zone is new in British ecology. It obviously corresponds with the dwarf shrub zone of *Empetrum-Vaccinium* of Scandinavia and Switzerland. In the early surveys of British vegetation by the Smiths, which incidentally did not include the Cairngorms, no distinction was made between the Vaccinieta of the high altitudes (3000 ft. and over) and those falling within the altitudinal limits of the *Calluna* zone. This failure to make the separation is not surprising in view of the shortage of differentiating species, the chief being *Empetrum hermaphroditum* and *Vaccinium uliginosum*.

At the time of the early surveys, *Empetrum hermaphroditum* was not distinguished from *E. nigrum*, and details of their distribution are still incomplete. But in general *E. nigrum* occupies the lower slopes and *E. hermaphroditum* the upper to the summits with some overlap in the middle. *E. hermaphroditum* is rather patchily distributed, being absent from the most exposed places in the *Juncus* belt but occurring within it in protected places between boulders. It can withstand more exposure than *Vaccinium myrtillus*, being a codominant with *Calluna* in the ecotone of exposed places between the *Calluna* and *Empetrum-Vaccinium* zones. Near the very top of the cone-shaped Mt Keen (3070 ft.) it forms an almost pure community. Like *Vaccinium myrtillus* it can withstand long-persisting snow-cover.

According to Trail (1895) *V. uliginosum* is found in the Cairngorms 'very local in bogs, at altitudes from about 1800 to 3500 ft.'. But according to our observations its range is from 1800 to 3700 ft.; its distribution is patchy and it is primarily a plant of the *Empetrum-Vaccinium* zone. It is, however, most luxuriant, though local, on steep sheltered rocky banks at much lower altitudes, e.g. 2200-2400 ft. Here it flowers freely, whereas it is usually sterile in the higher communities.

The high-altitude Vaccinietum of the Smiths and the 'Alpine *Vaccinium* heath' described by Crampton & Macgregor (1913) from Ben Armine in Sutherlandshire are considered to belong to the *Empetrum-Vaccinium* zone. On Ben Armine it occurs at the low altitude of 2250 ft., and bears the same habitat relations of exposure and snow-cover to Callunetum on the one hand and Rhacomitrietum on the other as these communities bear to each other on the Cairngorms. The community on Ben Armine includes *Vaccinium uliginosum* and *Cetraria islandica*, but whether the *Empetrum nigrum* recorded is really the species or the subspecies *E. hermaphroditum* is not known.

In the oceanic conditions of the extreme west some alpine species descend to sea-level.

It appears as if the sharper differentiation which characterizes the zones of the continent finds its nearest approach in this country in the severe climatic conditions of the Cairngorms massif. Here, if anywhere in this country, one might be able to recognize a well-defined *Empetrum-Vaccinium* zone.

Juncus *zone. Juncus trifidus* descends to a lower altitudinal limit of about 2400 ft. Above this level it is a component of most communities. It can stand long burial by snow, being absent only from those areas where the snow lies longest; it is also absent from the wettest places. It is, however, the characteristic species of exposed slopes above 3200 ft. and summit plateaux. In the Cairngorms such areas occupy many square miles.

The characteristic and most widespread community is Juncetum trifidi of exposed situations and coarse gravelly soil with numerous subangular boulders embedded in it. The tussock form of *Juncus trifidus* characterizes several of its associates; of these, *Deschampsia flexuosa* is the most widespread, varying much in frequency from occasional to locally dominant. The critical factor determining its density and local importance appears to be edaphic rather than microclimatic, although its exact nature is unknown.

Although *Juncus trifidus* is the most widespread species of these inhospitable summit plateaux, *Carex rigida* is the characteristic species of mean conditions at high altitudes. Although rare in the Juncetum trifidi it becomes increasingly abundant with increasing shelter and snow-cover, and in the Caricetum rigidae dominates quite considerable areas of ground sloping gently eastwards on Braeriach and Cairn Lochan plateaux.

In slightly more exposed places *Carex bigelowii* shares dominance with *Rhacomitrium lanuginosum*. This combination of dominance is rather sparsely represented in the area examined, but it covers the flat summit of Glas Maol. A brief examination of the community shows small patches of *Carex bigelowii*, of *Rhacomitrium lanuginosum* and of *Deschampsia flexuosa* with *Festuca ovina*, and the phenomena strongly suggest a cycle of change in which the last two species colonize the patches from which *Rhacomitrium* has been eroded.

Interesting problems of their origin, maintenance and present status are raised by the occurrence on Cairn Lochan of 'islands' of a *Carex-Rhacomitrium* community set in a 'sea' of Juncetum. There are several of them, all roughly the same shape, about twice as long as they are broad, the long axis perpendicular to the prevailing wind, and all raised above the general level of the erosion pavement by a few inches of sand, higher on the eroded western side and lower, almost flush with it, on the leeward side.

Snowfields and snow-patches. The only essential point of difference between the snow-field and the snow-patch is the duration of the snow. In both, snow lies late, but in the typical snow-patch the snow is 'permanent', and only on rare occasions does it melt sufficiently to uncover soil devoid of vegetation. Diagrammatically the recession of the edge of the snow-patch uncovers ground exposed for progressively shorter periods. At the same time the melt water irrigates the zone next the receding edge. A series of concentric rings of plant communities is the result.

Many factors complicate this oversimplified scheme. In and around the snow-bed the terrain is often much broken, slopes vary in steepness, the 'soil' varies from a fine mud to coarse gravel, boulders or bare rock, the water may be from springs arising below the snow-bed and irrigating alluvial terraces on the banks of the resultant streams, or it may come from melting snow; its amount and duration, and the extent of the ground irrigated by it vary. Ultimately, however, the most important factors appear to be the duration of

the snow-cover and the amount and duration of an effective water supply. A typical picture such as is presented by Margaret's Coffin is a basin with *Nardus stricta* dominating the rim. An intermediate belt showing the progressive reduction in *Nardus* and the increasing importance of bryophytes consists in its outer part of a patchwork of *Nardus, Carex bigelowii, Deschampsia flexuosa* and some *Salix herbacea* and in its inner part of patches of the last three species with generally distributed and abundant *Gnaphalium supinum*. The central core of bryophytes has an outer zone dominated by *Dicranum* spp. and an inner by *Webera ludwigii* exposed when the snow had almost disappeared in September 1948.

Besides the local terrain two further factors may help to explain the complexity of the vegetation of late snow areas in the Cairngorms. Several areas show a patchwork of the dominants *Nardus stricta, Carex rigida* and *Deschampsia flexuosa*. A brief examination of the relations between these species in such patchworks on Lochnagar strongly suggested that we are dealing with the phenomena of cyclic change. The normal course of a cycle of change would itself be affected by two of the most powerful factors in the habitat, namely, snow-cover and water supply from melting snow. Variation in these from year to year would produce conditions which may be assumed to favour now one dominant, now another. But further investigation is needed to unravel the causes of the complexity.

The status of, and the relations of these dominants to *Salix herbacea*, also need fuller inquiry, for although *Salix herbacea* is a constituent of communities in the *Juncus* zone, and although it may be locally common in those communities uncovered late in the season, its dominance in the snow-patches investigated is of very limited extent.

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THE ECOLOGY OF THE LOUGH INE RAPIDS WITH SPECIAL REFERENCE TO WATER CURRENTS

I. INTRODUCTION AND HYDROGRAPHY

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(With Plate 23 and nine Figures in the Text)

CONTENTS

A. INTRODUCTION

One of the chief obstacles in the ecological study of the littoral and shallow sublittoral regions of the sea coast is the difficulty of disentangling the effects of many environmental influences all varying in intensity from place to place and thus acting together in different combinations. For this reason a thorough ecological survey of any area is usually a formidable undertaking: the recognition of the essential environmental factors is by no means assured; the sorting and identification of material are most laborious; and the resulting data may not be adequate for interpretation except in vague terms. Some of these difficulties have been avoided by workers who have confined their attention to one particular animal at a time, studying it over a wide area; and many successful investigations have resulted from this method. Another approach to this problem is to choose an unusual locality in which one obvious factor (or group of inter-dependent factors) varies very strongly from place to place, while others vary only slightly, at any one time, throughout the area. Although we cannot expect to find the perfect locality, some places are much more suitable for this kind of investigation than others. For instance, the study of intertidal rock surfaces can be greatly simplified by the selection of places where the slope is uniform (Kitching, 1935). These various considerations led us to the study of the Lough Ine Rapids, an area specially suitable for the study of the effects of water current on coastal marine organisms. The potentialities of this locality were well recognized by Prof. L. P. W. Renouf of University College, Cork, who established the marine biological laboratory which has formed the base for the field work described in this and succeeding papers.

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Lough Ine (Pl. 23 A) is a marine lough near the western end of the south coast of Ireland. It opens southwards through a narrow channel, known as the Rapids, into Barloge Creek, which itself opens into the Atlantic. An account of the district, with photographs and maps, has already been published in this *Journal* by Renouf (1931). Lough Ine (Pl. 23 A) is about 1 km. long and at one spot 50 m. deep. The 'Rapids' are about 150 m. long and are 12 m. wide and 1 m. deep (at low tide) in their narrowest and shallowest part, which is known as the 'Sill'. The inrush and outrush of water through the Rapids, due to the rise and fall of the tide in the sea, produce currents reaching 2–3 m./sec. (4–6 knots) in the region of the Sill. The fauna (Renouf, 1931) and flora (Rees, 1935) of Lough Ine are typically marine. It is probable that the salinity falls within the usual range for coastal waters (see p. 318); very little fresh water runs into the Lough, while the exchange of water due to the tide must be considerable. The bottom and shores of the Rapids are rocky.

The object of the investigation described in this series of papers is an ecological study of an area comprising the Rapids and the adjoining portions of Lough Ine and Barloge Creek. Some knowledge of the hydrography, and especially of the water currents, is an essential basis for such a study. Having gained this we may investigate the distribution of animals and plants by comparing the populations of the region of strongest current on and near the Sill, of the regions of moderate current north and south of this, and of regions of relatively quiet water which are provided by several small creeks and bays. Finally, after determining the distribution of the commoner animals and seaweeds, we hope by means of field experiments to investigate the ways in which water currents act on some of these organisms.

The investigation of the Lough Ine Rapids is being carried out by means of short annual summer expeditions organized from and supported by the Department of Zoology of the University of Bristol. The research programme is planned and conducted jointly by the four authors as senior members of the party, assisted in the field by from six to twelve students* from the Department. Scientific preparation for the expeditions and organization of the daily programme in the field is the responsibility of one of us (J.A.K.), while another (F.J.E.) is responsible for all executive arrangements for travel, camping and commissariat.

B. TOPOGRAPHY

Methods

Since the existing 25-inch-to-the-mile Ordnance Survey map was insufficiently detailed, it was decided to make a new map (Fig. 1) of the area under study. The west bank of the Rapids, which is formed by a stone quay, was chosen as a base-line. The edge of the quay was marked at 10 m. intervals, which were measured with relation to a fixed iron ring. This gave a series of points marked 1–7 on the map, the edge of the quay adjacent to the iron ring coinciding with point 3. This base-line was produced southwards, and at

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* The following took part as students in the field work described in this paper: in 1938, S. Bennett, Jean M. Fry, H. Gorvett, J. S. Hellier, D. A. Parry, Ruth Parry, H. F. Steedman, Nita Wigmore; in 1946, Avice Brindley (St Andrews), Betty W. Knight, Sylvia J. Lilly, Constance Plaice, Patricia E. Wade; in 1947, Mary Day, Estelle Davies, J. B. Gilpin-Brown, Mary Harrison, Mary Hay, D. Johns, Sylvia J. Lilly, Elizabeth Manners, Margaret Manning, Rachel Noble, Constance Plaice. Catering was carried out by Phyllis Whitton in 1946 and by Diana Purchon in 1947.
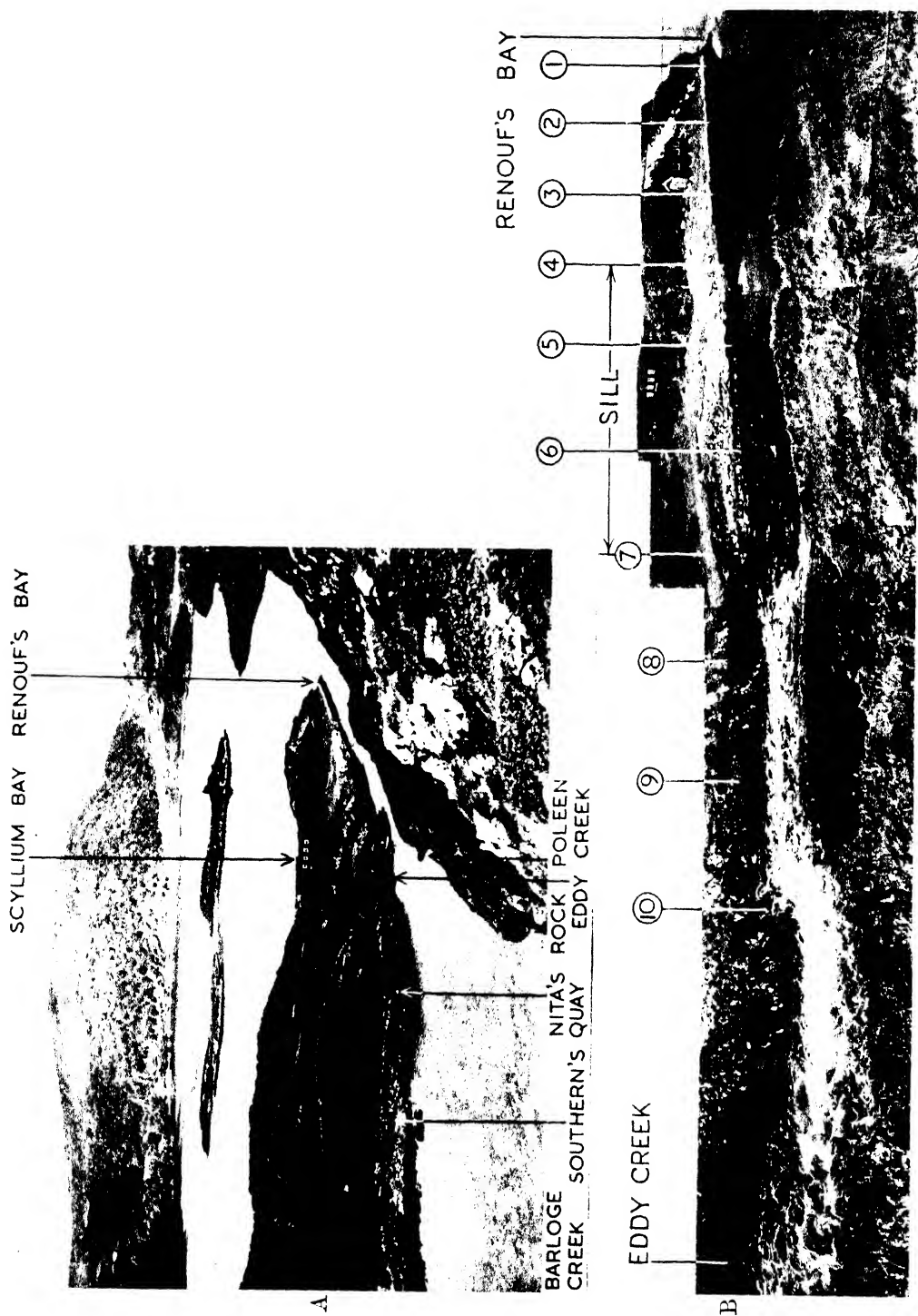
Phot. A. A view from Barloge Creek of Lough Ine during outflow in the Rapids. Phot. F. J. Ebling.

Phot. B. A composite photograph of Lough Ine.

10 m. intervals perpendiculars were drawn to meet the high-water line at points 8, 9 and 10. Corresponding points on the east bank were established on the high-water line at 90° magnetic (1947) from points 1 to 10, giving a series of ten traverses across the Rapids. The area was mapped from these points with a prismatic compass and where suitable by linear measurements.

For reference purposes the map has been subdivided by the construction of a metre grid, oriented with respect to true north, so that it is possible to specify any point in the area by means of two co-ordinates, one east of zero and one north of zero, both expressed in metres. Point 3 was designated East 100, North 200, i.e. 100200 in grid notation.

Place names were used as they appear on existing ordnance maps or after Renouf (1931); in some cases local names not previously recorded were used, and failing this names were given by members of our own party.

The submarine contours were constructed from soundings made over a number of sections traversing the area. These soundings were made at low or high slack water of measured level, and were reduced to an arbitrary standard level 157 cm. below the edge of the quay at point 3. This level is approximately that of low slack water (low water in the Lough). The level of low water of spring tides at Nita's Rock (Barloge Creek) was approximately 160 cm. below this standard level.

The coastline mapped was that of high-water mark of spring tides. The low-water line was also mapped and is shown as a dotted line; seawards of the Sill this indicates the low-water line of spring tides, but above the Sill that of neap tides, thus representing in each case the lowest level reached by the water in these two areas as will be explained in the hydrographical section.

Description of area

The Rapids (Pl. 23 B) connect with Lough Ine at their north end and open into Barloge Creek at their south end.

At the north end of the quay which forms the west bank of the Rapids is a boat slip opening into 'Renouf's Bay'. Farther west along the shore of the Lough lies Scyllium Bay, near which the main laboratories are situated. Tide measurements for the Lough were made at a point (Peggy's Mark) on the coast between these two bays.

South of the quay the west bank forms successively a bight between points 8 and 10 and a sheltered bay known as Eddy Creek; then it curves west to Southern's Bay. Tide measurements for Barloge Creek were made at 'Nita's Rock' at the north end of Southern's Bay. South of this there is a projecting quay.

On the east bank, at the north end of the Rapids, there is a small harbour. South of the Rapids, where they open into Barloge Creek, the east bank forms a bay known as 'Poleen'.

The west bank of the Rapids is vertical in the region of the quay, and shelves moderately in the region south of it. Eddy Creek has steep sides, but a fairly flat bottom. The east bank of the Rapids, from the harbour southwards to traverse 10, shelves very gently; at low water a zone of boulders between traverses 6 and 9 is left awash. Farther south the bank is steep.

The maximal depth (measured below standard level) of the north part of the Rapids is between 1·5 and 2·0 m., and occurs along a line about 7 m. from the west bank. The bottom in this region is covered with boulders. Between traverses 4 and 6 the maximal depth is little more than a metre; while from traverse 7 southwards it increases rapidly.

The shallow region between traverses 4 and 7 is termed the 'Sill'. These features are illustrated by longitudinal and transverse sections shown in Fig. 2.

C. HYDROGRAPHY

(i) *Introduction*

In order to make possible an appreciation of the conditions of life in the Rapids area, an investigation has been made of the physical conditions, particularly of the water currents. The general picture obtained is presented in the following subsections of this paper.

(ii) *Tidal levels: preliminary account*

Tidal conditions in Lough Ine have been described briefly by Renouf (1931) and Rees (1935) from work carried out by the Engineering Department of University College, Cork. Our own observations in general agree, although we believe that certain additions and modifications are necessary.
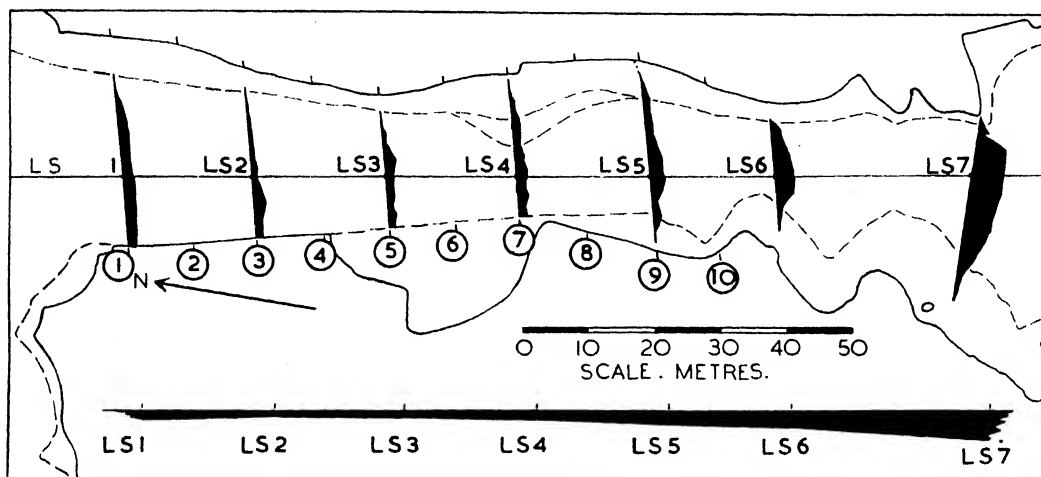

Fig. 2. A map of the Lough Ine Rapids showing the line of the longitudinal section (LS) and stations LS 1–7. Map stations 1–10 are also shown (in circles). The depths below standard level of the cross-sections at stations LS 1–7 are indicated by the black diagrams (with a depth scale equal to the horizontal scale). A similar diagram (below) gives the depths along the longitudinal section. The transverse section shown at stations 1 and LS 1 is the one used for the current measurements described in subsection (vi) and Table 1.

At the south end of the Rapids (off Nita's Rock) the water in Barloge Creek rises and falls with the sea in a normal tidal rhythm, having a range of $3\frac{1}{2}$ m. at spring tides and of about $2\frac{1}{2}$ m. at neap tides. Within the Lough (and in the northern part of the Rapids) the tidal conditions are profoundly modified by the Rapids and in particular by the Sill. The Rapids act as a resistance to the flow of water, so that the tidal rise and fall in the Lough lags behind that in the sea (Fig. 3 A). Actually the range of spring tides in the Lough is about 1 m. and of neap tides about $\frac{2}{3}$ m. There are two other interesting anomalies: the water in the Lough falls to a lower level at neap tides than at spring tides (Fig. 3 B), and the duration of outflow in the Rapids is about double that of inflow. These phenomena are best understood from a consideration of the data presented in the next subsection.
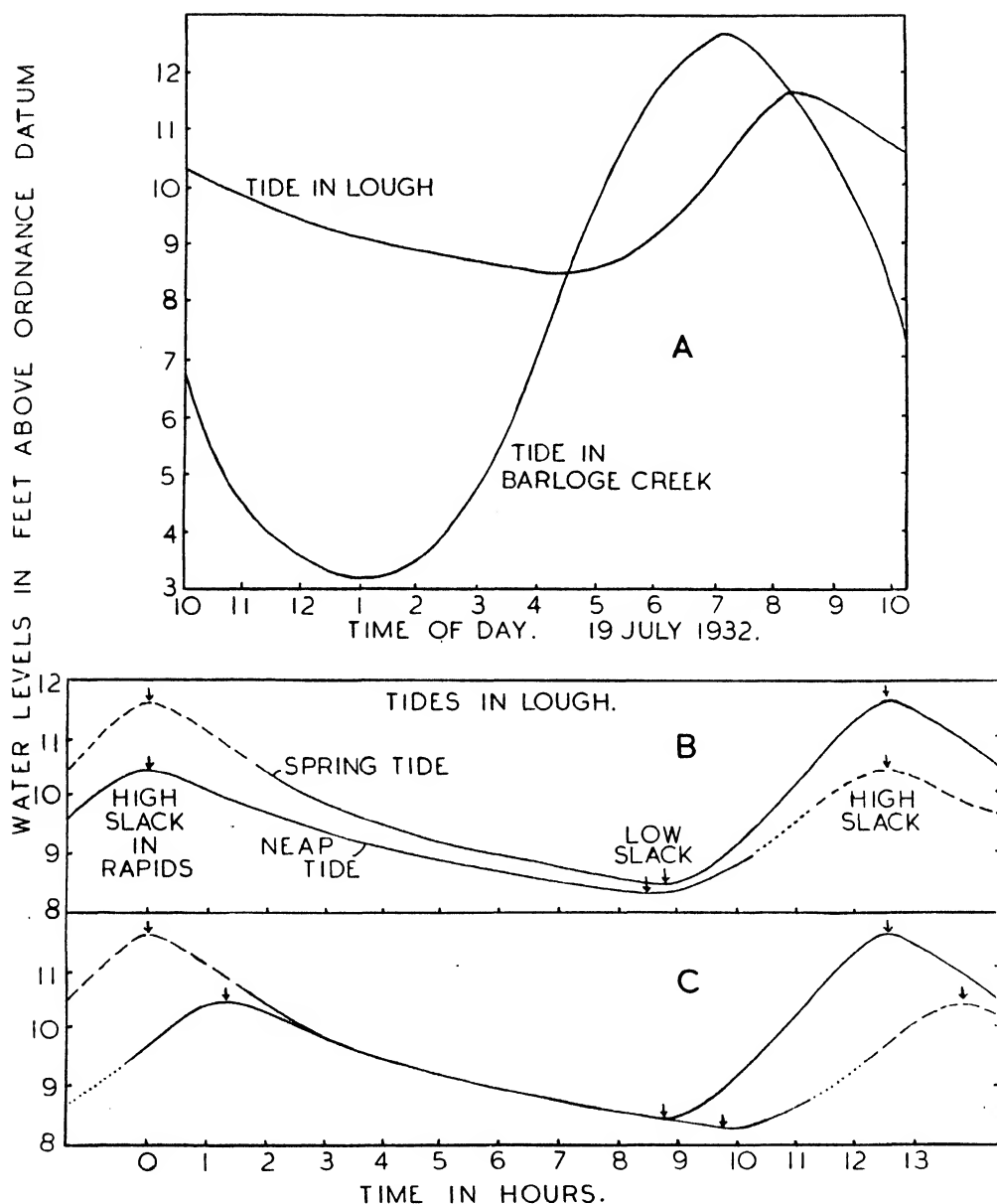
Fig. 3. Graphs showing the rise and fall of water level in Lough Ine and Barloge Creek. A. Tide levels for spring tide in Lough Ine and Barloge Creek on 19 July 1932. B. Tide levels for neap and spring tides in Lough Ine with the times of high water made to coincide. C. The same curves in B with the neap tide curve displaced to the right so as to superimpose the curves for about 6 hr. of outflow. (Figs. 3 A and B are copied from curves published by Rees (1935, Graph 2), made from data originally provided by Prof. H. N. Walsh of the Engineering Department, University College, Cork. In order to produce the complete curves in B and C it was necessary to repeat part of Rees's curves. These parts are shown by broken lines. The dotted parts were inserted to give smooth curves.)

(iii) *Water movements in a longitudinal section of the Rapids*

As a basis for an understanding of the hydrography, the water currents were measured at various states of tide along a longitudinal section of the Rapids. The longitudinal section was chosen so as to lie along the deepest part of the channel and in the full current.

A suitable line for the longitudinal section was first drawn on the map (see Fig. 2). In order to specify its position a traverse was drawn across Barloge Creek at 90° magnetic (1947) from the east corner of Southern's quay. The longitudinal section was found to intersect this traverse at 45 m. from its origin, and also to intersect traverse 1 at 11 m. from point 1. These traverses were then marked out in the field by means of ropes, and the longitudinal section fixed by measurement. A yellow marker was placed at the intersection of the longitudinal section and traverse 1, and a white mark was painted on the shore of the Lough in line with the longitudinal section. A boat in the Rapids could then be brought into position on the longitudinal section by alinement with these two marks. The compass direction of the longitudinal section was found by field measurement to be 5° magnetic, thus agreeing with the line on the map.

Measurements of current were made with a Watts current meter fixed on a pole and held well away from the boat. The boat was held in position by ropes from each bank—an undertaking which on occasion required the full strength of the party. Measurements were made in duplicate at various depths at each of a series of stations (LS 1–7) on the line of the section. (The designation of these stations is not the same as that of the traverses.) These stations were worked in rotation throughout the tidal period, the water level at the adjacent shore mark being recorded in each case. Bad weather interrupted observations on 15 July 1947, but the work was completed on the next day after a similar state of tide had been reached. It was not possible to obtain readings near the bottom owing to the canopy of long brown algae which interfered with the rotating cups of the Watts meter.

An analysis has been carried out by which the numerous readings of current speed, taken successively throughout the day, have yielded a series of contoured diagrams of current strength throughout the section, each representing a selected stage of the tidal cycle. The method of analysis is illustrated in Fig. 4 for the data from station LS5. Each station was worked six times during the tidal cycle. The six sets of current readings (two for inflow and four for outflow) taken at station LS5 were plotted with relation to height above bottom in Fig. 4 A. From this graph current speeds were read off for selected levels and were plotted on a time scale, as shown in Fig. 4 B. In addition to the six readings for each level obtained in this way, two more were available for the occasions of slack water, when there was no current. The lines in Fig. 4 B are thus each based on eight readings, and cannot be regarded as giving more than a general indication of conditions. From the series of figures similar to Fig. 4 B (one for each of the seven stations), it was then possible to read off current speeds at fixed levels for any time during the tidal cycle. The times chosen were at 1, $2\frac{1}{2}$, $4\frac{1}{2}$, 6 and $7\frac{1}{2}$ hr. of outflow (i.e. after high slack water) and at 1, 2 and 3 hr. inflow (after low slack water). The resulting figures are expressed graphically in Fig. 5 on a much exaggerated vertical scale.

The following sequence of events may be deduced from the sections in Fig. 5. After 1 hr. of outflow the level in the sea (to the right in the figure) has fallen below the level in the Lough, and water is flowing out at a fairly rapid rate, attaining a speed of over
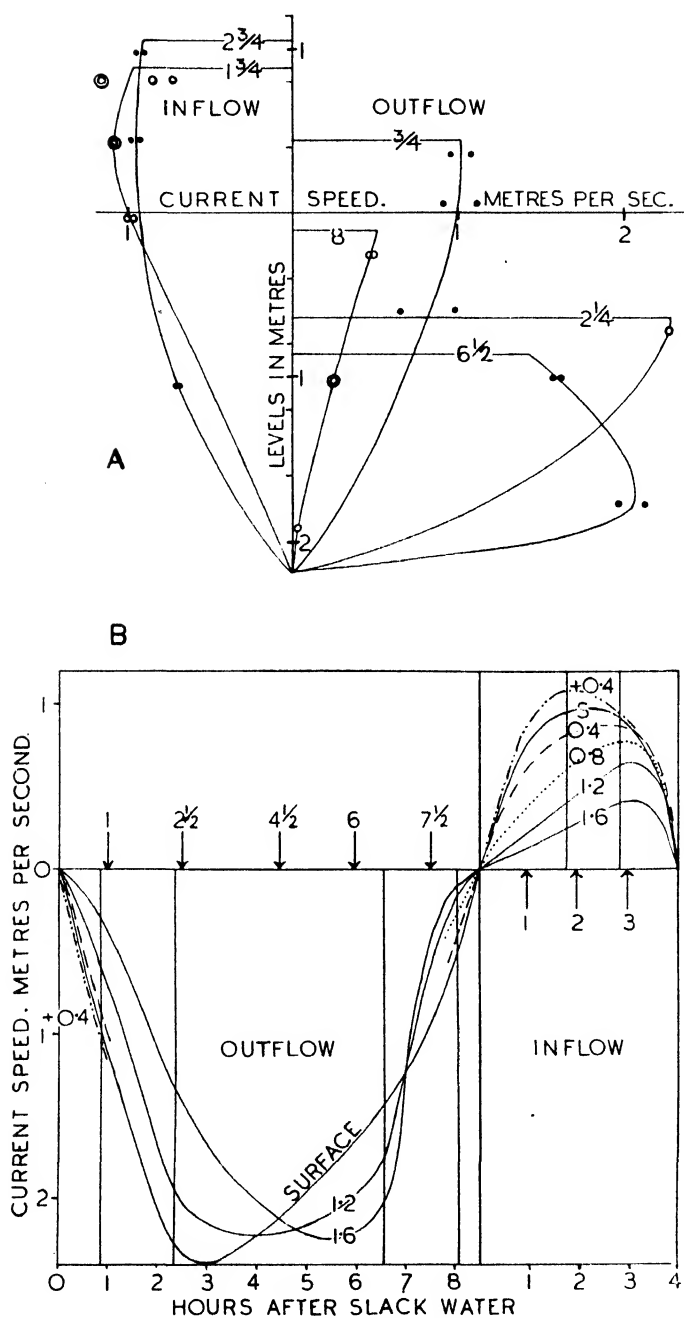
Fig. 4. Graphs illustrating the methods of analysis of readings of current strengths. The data plotted above are for station LS5. A. Current measurements made at different levels plotted with reference to the standard level. Each of the six curves represents readings taken at one part of the tidal cycle, and the numbers refer to hours of inflow (to the left of the vertical axis) or outflow (to the right). B. Current speeds for specific levels plotted against time. These curves were derived from Fig. 4 A. Specific levels are marked on the curves in metres below standard level except for +0·4 which is above standard level.

2 m./sec. at the narrowest and shallowest part, over the Sill. As the level in the sea continues to fall (after $2\frac{1}{2}$ and $4\frac{1}{2}$ hr. of outflow) the rate of flow rises to a maximum of 3 m./sec. in the surface layers, but the amount of water passing appears to be limited by the steep and relatively shallow stretch immediately south of the Sill. This stretch of water, between stations LS3 and LS5, will be shown below to be acting by this time as a 'control section'. After 6 hr. of outflow the control section is still limiting the rate of flow, and the distribution of current is similar to that after $2\frac{1}{2}$ and $4\frac{1}{2}$ hr. of outflow; but the level in the sea is now rising. After $7\frac{1}{2}$ hr. of outflow the rise in level of the sea has been so great as to reduce the flow; and after $8\frac{1}{2}$ hr. (not shown) the levels in the sea and the Lough coincide so that the water stands for a moment ('low slack water'). However, the level of the sea is rising very rapidly, so that the current quickly reverses and water pours into the Lough (1, 2, and 3 hr. inflow). Owing to the narrowness of the Rapids the rise in the Lough lags behind that in the sea. High tide in the sea is reached after about 3 hr. of inflow, and the water there now falls, but owing to the lag caused by the Rapids the level in the Lough is still substantially lower, so that water continues to flow in even though the tide is falling outside. Only after about 4 hr. do the rising level in the Lough and the now falling level in the sea coincide, giving 'high slack water'. As the sea level falls still further water begins to flow out of the Lough, and another cycle begins.

In summary, high water in the Lough is later and somewhat lower than high water in the sea, and coincides with high slack water (i.e. the turn of the current) in the Rapids, while low water in the Lough is later and higher than low water in the sea, coinciding with low slack water in the Rapids. Actually the level of low water in the Lough is slightly above that of half-tide in the sea. Since the level of water in the Lough fluctuates only within the upper half of the tidal range of the sea, it is natural that outflow in the Rapids should last much longer than inflow. The actual times are about $8\frac{1}{2}$ hr. for outflow and about 4 hr. for inflow.

(iv) *Tide levels in Lough Ine in relation to the 'control section'*

During the greater part of outflow—that is between $2\frac{1}{2}$ and $6\frac{1}{2}$ hr. after high slack water, as illustrated in Fig. 5—the stretch of the Rapids immediately to the south of the Sill, from station LS3 to station LS5, is much steeper, shallower and narrower than the rest. It is suggestive, imperfectly of course, of an inclined open gutter draining into a trough. In such a system the rate of flow of water in the gutter is dependent, among other things, on the head of water from which it is fed, but not on the depth of water in the trough. The extent to which the Rapids approach such an idealized system can be tested from the data for tidal levels published by Rees (1935). His graph for the tidal rise and fall in the Lough and sea at spring and neap tides is reproduced in our Fig. 3 A. It will be seen from Fig. 3 C that by a shift along the time scale the curves for the fall of the tide in the Lough at spring and neap tides can be made to coincide for the greater part of their lengths. Thus, after the level of water in the Lough drops to about 10 ft. above ordnance datum, further fall follows the same course, irrespective of the level of water in the sea.

A consideration of this 'control section' effect led us to question the interpretation of tide levels in Lough Ine offered by Renouf and Rees. The low-water level of the Lough is lower during neap tides than during spring tides. Renouf (1931, p. 418) and Rees (1935, p. 72) have claimed that the lower level is attained because of the longer period of outflow during neap tides as compared with spring tides. This explanation may in part and for

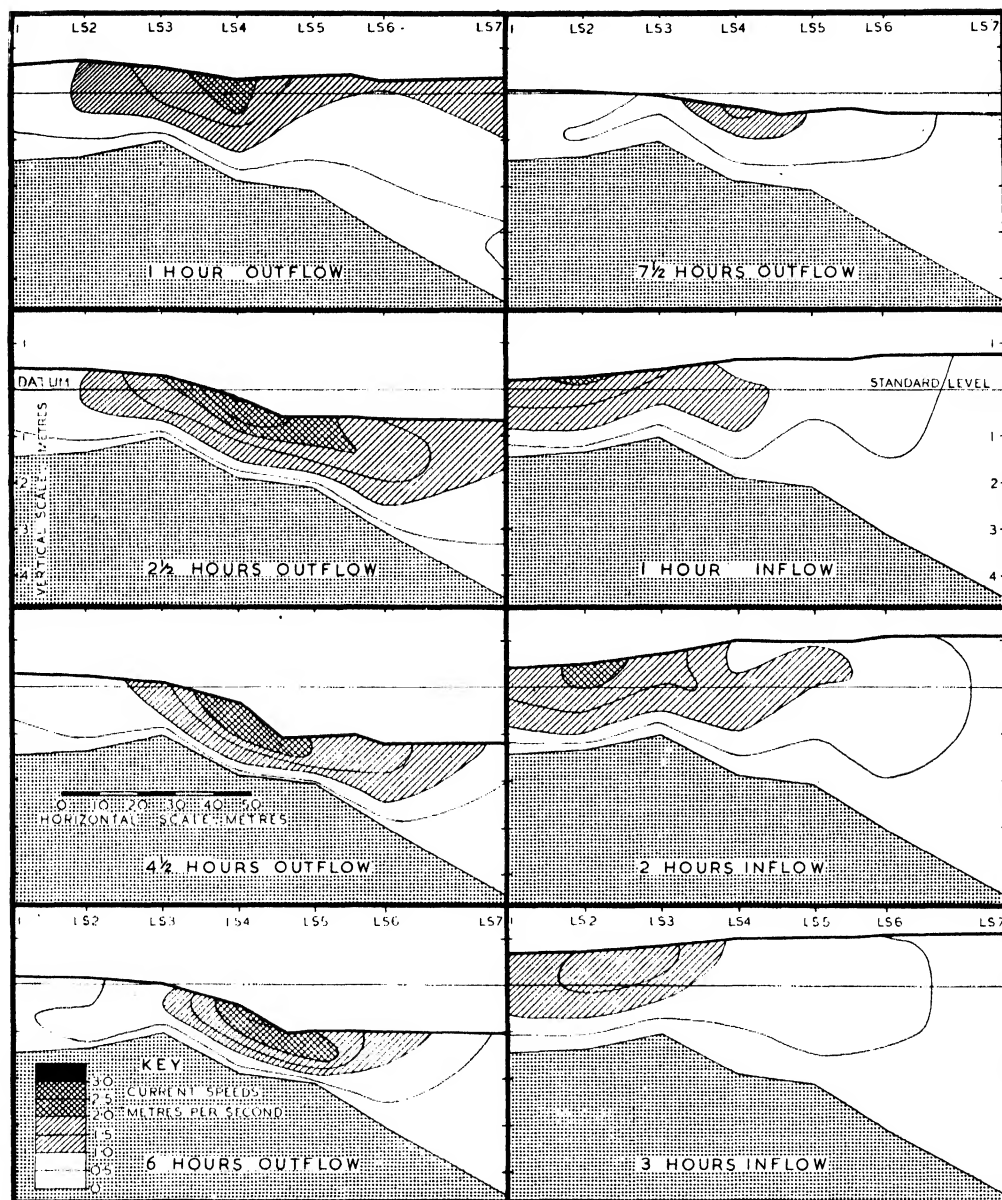Fig. 5. Current speeds along a longitudinal section of the Lough Ine Rapids and at different states of the tide. These data were read off from the speed-time graphs of the individual stations of which Fig. 4 B is an example. (Similar curves were available for stations LS1–7.) Water levels were read when current measurements were taken. In these diagrams the Lough is to the left and the sea to the right.

some tides apply to Lough Ine, but the data published by Rees do not support it. It is known that in some places the rise during spring tides may occupy less time than the rise during neap tides. This is a common feature in estuaries. Moreover, since the tidal curve (as illustrated in Fig. 3 A for Barloge Creek) must in any case rise more steeply at spring than at neap tides, the water will reach any given level above mid-tide level earlier in the tidal period at spring tides than at neap tides. However, if the curves given by Rees (1935, Fig. 2) for the tidal cycle in Lough Ine are redrawn so that the times of high water for spring and neap tides coincide (Fig. 3 B of our paper), it will be seen that (for the examples selected by him) the outflow is of slightly longer duration at spring tide than at neap tide. Further, since Rees has given the actual times of high and low slack water in his figure, it is possible to calculate these durations. They were 8 hr. 35 min. for the spring tide and 8 hr. 29 min. for the neap tide. (In obtaining the former figure we assumed that the tidal cycle at spring tides lasts 12 hr. 25 min. A comparison of the durations of the tidal cycle at Cobh (Queenstown) for July 1938 shows that there is no substantial regular difference between spring and neap tides in this respect.) Thus in the example quoted by Rees it is clear that the lower level attained in the Lough at neap tides is in no way due to a longer ebb. Nor does it seem likely that this explanation is ever of more than subsidiary importance. (See postscript on p. 321.)

An explanation of the lower level which is attained at neap tides in Lough Ine can be deduced from the superimposed curves for ebb given in Fig. 3 C. During spring tides much more water enters the Lough than during neap tides, owing to the much higher level attained in the sea. (There is, of course, no 'control section' effect during inflow, since the difference in the levels of water in the sea and Lough is not great enough to produce it.) Therefore at the beginning of ebb the water stands much higher in the Lough at spring than at neap tides. It will be observed from Fig. 3 C that the two curves begin to coincide—that is, the 'control section' effect starts to operate—when the water has been flowing out for 3 hr. during spring tides and for $1\frac{1}{2}$ hr. during neap tides. Thus owing to the lower level of high neap tide the falling water in the Lough has $1\frac{1}{2}$ hr. start by the time the curves coincide. The two curves thereafter follow the same course because of the 'control section' effect, until that for spring tides begins to rise again with the turn of the current. As a result the curve for neap tides has about $1\frac{1}{2}$ hr. during which it continues to descend below the lowest level achieved by the spring-tide curve. If it were not for the 'control section' effect the water in the Lough would fall more quickly at spring tides throughout ebb, because of a more rapid fall in the sea, so that ultimately a much lower level would be reached. The anomaly displayed in Lough Ine is a natural effect of the Sill. It is interesting that neap tides also ebb to a lower level than spring tides in the Severn estuary above Sharpness, though not in any part of the Tees. An explanation based on the greater entry of water at spring tides was also invoked in the former case (Bassindale, 1943).

(v) *Current in a transverse section*

An investigation was also carried out of the distribution of current strengths in a transverse section of the Rapids. The line chosen was that of traverse 1 (Fig. 2) across the northern end of the Rapids. Measurements were made in this transverse section at four stages of the tidal cycle on 23 July 1947. On each of these occasions readings were taken of the current at various depths at horizontal intervals of 2 m. all the way across

in rapid succession. The results for two states of tide are given in Fig. 6. It will be seen that the strongest currents occur at the surface and near the middle of the section. It was not possible to measure the currents in the lower parts of the section with the Watts meter owing to interference by the large brown algae.

(vi) *Total flow of water*

The amount of water passing through the Rapids in a given short period of time can be estimated from the data for the transverse section mentioned above and illustrated in Fig. 6. For this purpose the areas between adjacent contours were measured with a
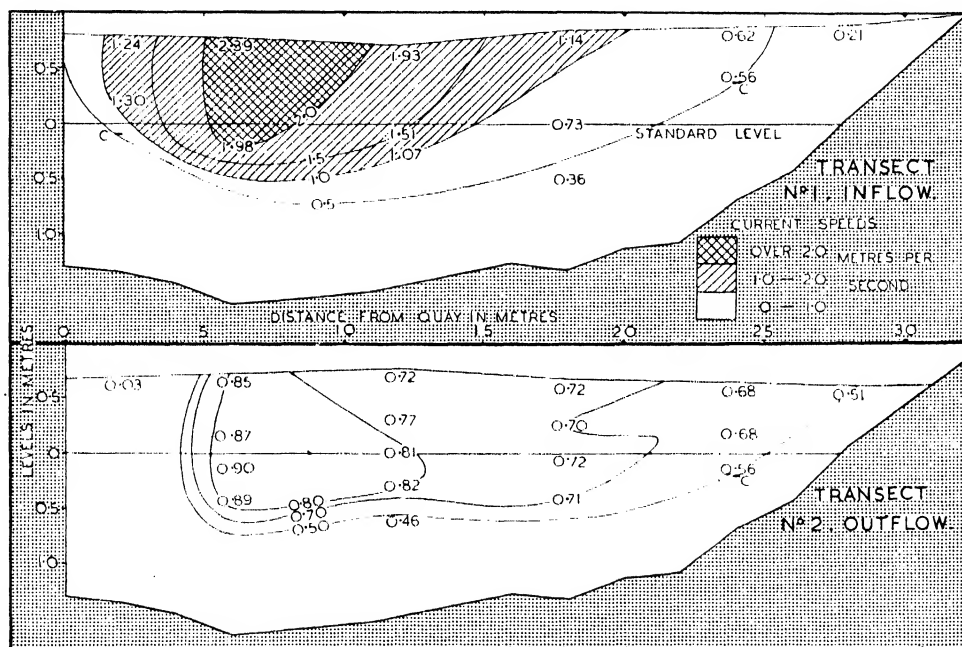

Fig. 6. Current speeds in metres per second in a transverse section at the north end of Lough Ine Rapids. Transect no. 1 was taken after 3¼ hr. inflow and transect no. 2 after 2 hr. outflow on 23 July 1947 (ordinary tide). Both were done in the section at traverse 1 (p. 307), which runs across from point 1 (Fig. 1). The levels marked *C* indicate the top of the canopy of brown seaweeds.

planimeter, and the average current speed appropriate to each of these areas was taken as the arithmetic mean of the two speeds represented by the limiting contours. In the case of the lowest region—between the bottom and the first contour—the mean current was arbitrarily taken as one-third of the speed represented by the contour, since this seemed likely to give a better estimate in view of the drag offered by the large brown algae.

The flow of water through the Rapids can also be estimated in another way. From the gauge readings of water level in the Lough (Fig. 7), which were taken on the same day as the readings of current in the transverse section, it is possible to determine the rate of rise or fall in level of water in the Lough at any particular time. From this and from the area of the Lough the amount of water entering or leaving in unit time can be determined for any stage of the tidal cycle. The area of the Lough was measured with a planimeter on

the 6-inch-to-the-mile Ordnance Survey map. It was found to be 0·506 sq.km. at low water and 0·542 sq.km. at high water; for intermediate levels an approximate adjustment was made between these limits.

The validity of this estimate depends on the water level falling at an equal rate over all parts of the Lough. As a check on this assumption, simultaneous readings of water level were made on gauges at both ends of the Lough. These are shown in Fig. 7. As the
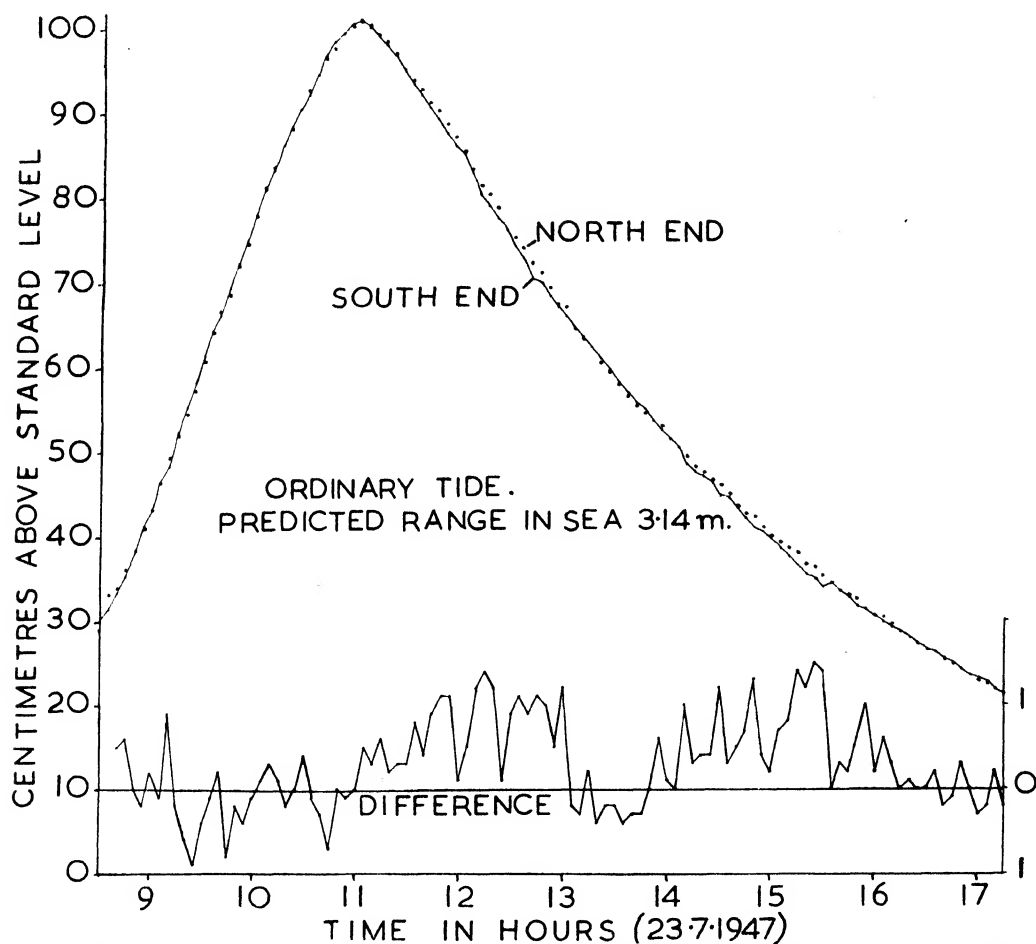
Fig. 7. Tide levels in Lough Ine on 23 July 1947. The upper continuous line represents the levels at Peggy's Mark (south end) and the dots show the readings at a quay at the north-west corner of the Lough. The relative levels of the two gauges were unknown; therefore the curves were arbitrarily made to coincide at high-tide level. The differences between the levels are shown below on an exaggerated vertical scale.

relative levels of the two gauges were unknown, the two curves have been drawn so that the levels of high water coincide. This may not be correct, but it enables a fair comparison to be made. The separation between the two curves is also shown on an enlarged scale (Fig. 7). It appears that there is a slight lag at the north end of the Lough, the level here tending to be lower during inflow and higher during outflow. The possibility also exists that there may be a rhythm in the variations of level. However, such discrepancies as occur are evidently on a small scale and probably do not seriously influence the results.

The estimates of total flow, obtained by the two methods outlined above, are given in Table 1. From the agreement between these figures it seems likely that they are reasonably correct. These results may be compared with those for certain rivers: for example, the mean annual flow of the Thames at Teddington for 1936–7 was 127 cu.m./sec.; the corresponding figure for the Severn at Bewdley was 71 cu.m./sec.; and the mean winter flow of the Tees in 1930 was 15 cu.m./sec.

Table 1. *The flow of water through the Rapids on 23 July 1947*

		Flow in cu.m./sec.		
		From current measurements	From areas of Lough and rate of change in level	Percentage difference
Time (G.M.T.)	Direction of flow in Rapids			
9.15 (¾ hr. before H.S.W.)	In	51·78	51·8	− 0·04
11.50 (2 hr. after H.S.W.)	Out	28·40	25·7	10·5
12.45 (3 hr. after H.S.W.)	Out	22·55	22·8	− 1·1
15.45 (6 hr. after H.S.W.)	Out	12·21	11·2	9·02

H.S.W. = high slack water.

(vii) *Surface currents*

As a preliminary to the measurements of current made with a Watts meter and described in preceding subsections of this paper, the surface currents over the whole Rapids area were determined and measured by means of floats. For this purpose bottles not quite filled up with water were timed over short measured distances. The results are summarized in Fig. 8. They support the data obtained with the current meter; and they clearly indicate that the maximal current strength occurs on the 'downstream' side of the Sill where the slope of the water is greatest, i.e. to the north of the Sill during inflow and to the south of it during outflow (compare Fig. 5).

In addition, the measurements made with floats reveal several features not discernible from the sections. Both during inflow and during outflow there is a weak eddy in Eddy Creek; and during outflow there is also a weak eddy off Nita's Rock. In Renouf's Bay the water is very quiet during inflow, since the main stream pours straight into the Lough in a direction parallel to the quay, thus leaving Renouf's Bay to one side; however, during outflow, the water is sucked from the Lough into the Rapids from all possible directions, and there is a weak but steady stream which sets across Renouf's Bay in a south-easterly direction.

Our observations of the surface currents have been fully confirmed by means of a tidal model of the Rapids area. This model was made out of concrete, to a vertical and horizontal scale of ½ cm. to 1 m. The water level in the 'sea' was caused to fluctuate in an appropriate tidal rhythm by the rise and fall of a large partially submerged displacing body, the movements of which were operated electrically by means of a connecting rod and driving wheel. It was found convenient to operate the tides on a time scale of 10 sec. representing about 1 hr. In response to this tidal rhythm in the 'sea', inflow and outflow were set up in the 'Rapids' with the currents qualitatively as described above, and the relative durations of flood and ebb in the 'Lough' were faithfully reproduced. The maximum of

current speed on the downstream side of the Sill, the eddies in Eddy Creek and off Nita's Rock, and the peculiar conditions in Renouf's Bay, could all easily be seen with the help of particles floating on the surface of the water. The model thus confirms the field observations.
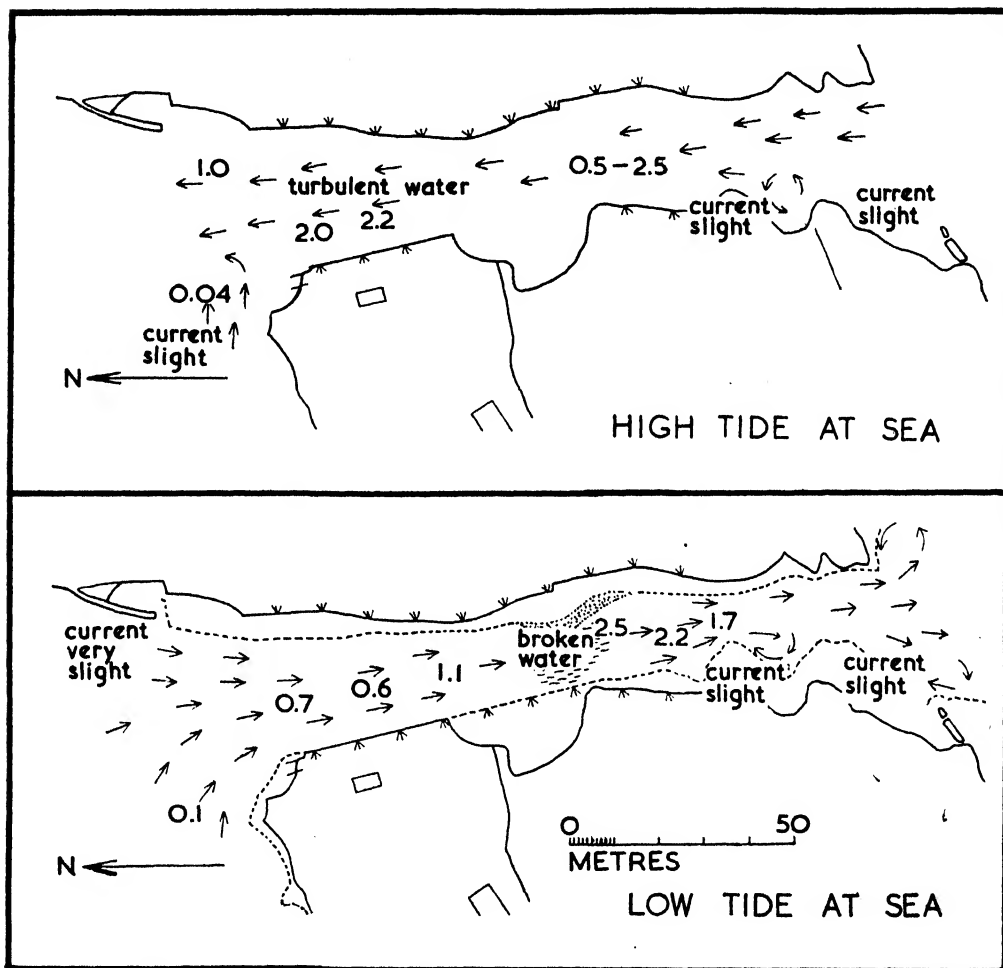
Fig. 8. Charts of the surface currents of the Lough Ine Rapids (in metres per second) as determined by the timing over short distances of surface floats. July 1938. Above: during inflow. Below: during outflow.

(viii) *Other factors*

From the point of view of the distribution of animals and plants in the Rapids area it may confidently be assumed that any major change in the salinity, oxygen content, acidity, temperature, or other attribute of the water will affect all parts equally. In this connexion it may be pointed out that measurements of water density made by Renouf in September and April indicate salinities of 37·5 and 33·5 parts per thousand respectively at the surface of the Lough, although the pH remained at 8·4. Also we have shown that temperatures vary with the state of tide (see further).

Despite the general assumption, however, that these major variations will affect all parts of the Rapids area, there is some indication of local minor variations which may have an important bearing on the distribution of animals and plants in places with relatively weak currents.

On 15 July 1938 surface temperature was measured along the west bank of the Rapids at intervals throughout the day. The thermometer, graduated to $\frac{1}{10}$th degree and previously standardized, was read while held immersed. The positions chosen were well outside the fringe of littoral algae. During the morning the sky was mainly overcast with occasional sunshine, but in the afternoon there was strong sun. The wind was light to moderate from the north-west. The results are given in Table 2.

Table 2. *Surface-water temperatures at stations along the west bank of the Lough Ine Rapids taken on 15 July* 1938 (*morning overcast; afternoon bright sun*)

			Temperatures (° C.) at stations					
Time (G.M.T.)	Tide in sea	Direction of flow in Rapids	Off Peggy's Mark	Off Point 1	Off Point 5	Off north point of Eddy Creek	Eddy Creek	Nita's Rock
10.25–10.40	Falling	Out	13·9	13·9	13·5	13·7	13·9	13·9
11.55–12.11	Falling	Out	15·1	14·2	13·9	14·0	13·9	14·5
14.26–14.35	Rising	Out	—	14·7	14·1	14·2	15·4	15·1
17.00–17.16	Rising	In	16·3	14·6	14·5	14·6	14·9	15·2
19.28–19.40	Falling	In	14·9	13·0	13·0	11·7	11·8	12·1

The results may be interpreted as follows:

(1) During outflow the temperature in the Rapids was determined by that of the water flowing out of the Lough. However, in the later part of inflow, colder water entered from the sea and produced a fall in temperature of 2 or 3°.

(2) In places protected from the main currents, as at Peggy's Mark, in Eddy Creek, and off Nita's Rock, the water was heated considerably by the sun.

It is clear that, if such effects as these can be observed in the case of temperature, then similar variations in other physical and chemical characters of the water may also take place. Where the whole area is affected—as by the drop in temperature at 19.30 G.M.T.— then all the animals and plants in the Rapids will feel the effect. But with local variations (as indicated under item (2) above) the distribution of organisms may be subject to influences other than those of water currents. This naturally will interfere with the interpretation of observations. However, even in these cases, the local variations in the conditions of the water are themselves dependent on a certain degree of freedom from water movement, so that the amount of current action is indirectly a controlling factor. Nevertheless, it is desirable that the extent of these variations in salinity, carbon dioxide tension, oxygen tension, acidity and temperature of the water should be investigated.

D. DISTRIBUTION OF DOMINANT SUBLITTORAL ALGAE

It is convenient to conclude this paper with a brief account of the distribution of the larger algae of the Rapids area, since some knowledge of this will be required for the remaining papers of this series.

The distribution of the dominant algae in the Rapids was plotted at or near slack water by observations from a boat in September 1947. The results of our observations are represented diagrammatically in the map in Fig. 9. Most of the area was covered with

laminarian algae, the fronds of which formed a dense 'canopy' (see Kitching, 1941). This canopy was held up high above the bottom only during the minute or two of slack water; normally the fronds were dragged downwards and sideways by the pull of the current. The most abundant component of the canopy was the large annual laminarian alga *Saccorhiza bulbosa,* which was found to dominate all parts of the area except as stated below. On the Sill itself *Saccorhiza* gave way to the perennial alga *Laminaria digitata.*
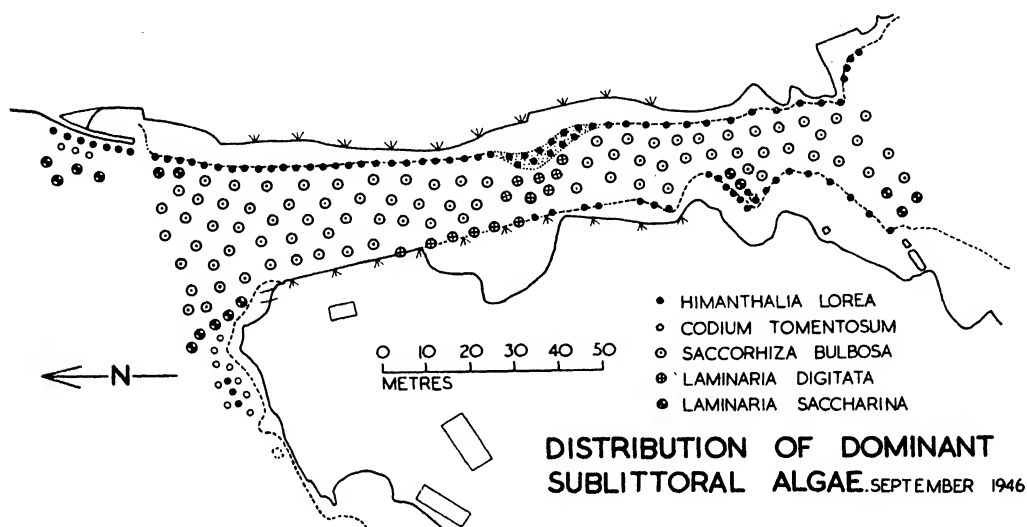

Fig. 9. Map showing the distribution of dominant sublittoral algae in the Lough Ine Rapids.

In those parts of the area least exposed to current, namely, off Nita's Rock, close inshore in the Poleen, in the inner part of Eddy Creek, near the Harbour, and in Renouf's Bay, *L. saccharina* covered the bottom. The alga *Codium tomentosum* was found to occupy much of the bottom in the shallow water along the shore just inside the Lough both near the Harbour and west of Renouf's Bay; it was more plentiful in 1946 than in 1937. The upper margin of the sublittoral region was fringed, except on the Quay, with a line of *Himanthalia lorea.*

SUMMARY

1. Lough Ine (Co. Cork, Eire) is connected with the sea by a narrow channel known as the Rapids, through which sea water enters and leaves with considerable force under the influence of the tide. This area thus offers outstanding opportunities for the investigation of the biological effects of water currents.

2. A detailed chart (Fig. 1) has been made of the Lough Ine Rapids.

3. The hydrography of the Rapids has been studied as a preliminary to the biological investigation. The resistance to water flow offered by the Rapids greatly modifies the tidal rhythm in the Lough (Fig. 3). It has been shown that during most of the period of outflow the Rapids act as a 'control section', so that the rate of outflow is independent of the level of water in the sea.

4. From measurements of current speed made with a Watts meter a series of diagrams (Fig. 5) has been prepared showing the current speed throughout a longitudinal section of the Rapids at various states of the tide. The fastest current was always on the down-

stream side of the Sill, that is, to the north during inflow and to the south during outflow. The highest reading obtained was 3 m./sec. (about 6 knots).

5. The total flow of water through the Rapids at various states of the tide has been estimated (Table 1) both from cross-sections contoured with respect to current strength and from observations of the rate of change of water level in the Lough. There was good agreement between results thus obtained. During inflow a rate of about 50 cu.m./sec. was attained.

6. Observations and measurements of surface currents (Fig. 8) have been made throughout the Rapids area, and these have been confirmed qualitatively with a working tidal model. There are well-defined eddies in certain parts of the Rapids area.

7. Although major changes in the physical and chemical characteristics of the water are likely to affect all parts of the Rapids area equally, there is evidence that minor deviations may arise in regions of quiet water (Table 2).

8. A map (Fig. 9) has been made of the distribution of dominant sublittoral algae in the Rapids area. Most of the bottom is covered with the large laminarian alga *Saccorhiza bulbosa*, while *Laminaria digitata* is dominant on the Sill and *L. saccharina* in places well out of the current. The fronds of the laminarian algae form a dense canopy.

POSTSCRIPT. Observations of the range of the tide and of the times of slack water made in July, 1948, have confirmed that the level of low water in Lough Ine is lower at neap than at spring tides. However, the duration of outflow was found to be slightly shorter at neap tides. These observations therefore show that variations in the duration of outflow do not account for the lower level of low water of neap tides in the lough.

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REVIEWS

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This number contains eight original papers, 11 reviews, and 121 Notices of publications on animal ecology of the British Isles, and occupies 100 pages. As usual, the papers are well spread over different groups of animals and various aspects of ecology. There are two dealing with general community distribution. J. R. Erichsen Jones describes his ecological surveys of four streams in the 'Black Mountain' district in South Wales. (This lies well west of the 'Black Mountains' themselves.) The streams differ in character a good deal; the fauna as a whole contained about 151 species, which are fully listed. L. S. V. and U. M. Venables made comparative counts of birds for two years in Kergord Plantations on Shetland, where the gradual acclimatization of trees and shrubs has brought about some marked increases in certain species of birds in recent years. Some, like the song-thrush and blackbird, are becoming commoner breeders, while others, like the wood-pigeon, previously passage migrants, show signs of stopping there to breed.

A much more general and abstract consideration of ecosystems, by A. Macfadyen, deals with the differences in significance between energy and matter circulating in plant and animal communities. It is pointed out that the energy is only used once, but the matter (the vehicle of the energy) often repeatedly. The total energy flow or 'activity' could be measured by the respiration rates.

The effect of different environments on a very simple community is described by T. B. Reynoldson, in a further contribution about the fauna of sewage filters. In these some interesting fluctuations caused by 'overgrazing' of fungal food supplies by fly larvae are mentioned, and also competition between fly larvae and enchytraeid worms. The question of competition and different feeding niches among fresh-water fish is analysed by P. H. T. Hartley, from a survey of fish food-habits in a Cambridgeshire river. He finds a definite overlap in feeding habits between various species, yet each has a distinct diet taken as a whole.

Helen Chitty gives the Canadian Snowshoe Rabbit Enquiry results for 1943–46, covering part of the downswing and following upswing of the ten-year cycle in numbers. The intrinsic natural rate of increase has been calculated for extremely few animals, and a paper by L. C. Birch is the first attempt to combine fertility and longevity data for an insect, and even here two species are combined to give a model of approximate increase. The great value of this paper lies in its development of the model and some conclusions drawn from it. David Lack applies to mammal litter sizes some of the ideas he has already used for clutch size in birds, his theory being that the upper limit is determined mainly by the ability of the mother to bring up a given number of young without increasing mortality.

Reviews deal with the recent White Papers on conservation in England and Wales, and in Scotland; the relation between insect outbreaks and the complexity of their biotic environment; species formation on Galapagos; animal communities of sea wrack in the Baltic and hot springs in Iceland; *The Indian Ecologist*, a new journal; an enquiry about ecological fluctuations from the Conseil International pour l'Exploration de la Mer; and books on British mammals, British insects, Practical field ecology and methods of keeping laboratory animals.   CHARLES ELTON

C. T. Prime and R. J. Deacock. *The Shorter British Flora.* Pp. 376 with 232 line illustrations. 1948. Price 12s. 6d. London: Methuen.

At a time when field study is so flourishing in Britain, the need for a good elementary flora is acute, but the difficulties to be overcome in achieving it are considerable. The authors have brought to their task great experience of school teaching in botany, and many admirable features of the book reflect this, namely, the comprehensive and clear glossary, the abundant and simple illustrations, the numerous and

straightforward keys. The format has been designed with great effectiveness and represents a great advance upon that of most available floras.

The book aims to permit the comparative beginner in the subject to identify the commoner wild flowers, by reference first to families, then to genera and to species; a short specific description is given of each species, and brief notes of general biological interest are appended in some instances. The whole is a large pocket book of 376 pages.

The feature which will naturally be most remarked upon as limiting the value of the flora is the restriction which the authors have made to about 750 British species of flowering plants and ferns. So far as one can judge, this selection will best suit the central and southern parts of Britain. A great many species which have been omitted are not so much generally rare throughout Great Britain as generally or locally common in some parts of it and absent or rare elsewhere; this is no doubt an inescapable disadvantage of which the authors are well aware.

It is inevitable in a book of this scope that despite the considerable trouble taken to secure competent advice there still should be room for correcting many minor errors. One notes that *Allium vineale* is reported as usually bearing no bulbils, a statement contradicted clearly by the account in the 'Biological Flora'; it is stated that all the *Pinus sylvestris* in England is from continental seed introduced at the time of the Napoleonic wars, whereas there is good evidence favouring the idea that much indigenous pine remains; *Nymphaea alba* is credited only with floating leaves.

Though the illustrations are valuable for their simplicity, they represent an aesthetic and scientific standard which could be much improved upon; the willow leaves are poorly drawn, the cucullate apex of *Potamogeton praelongus* is merely *not* shown in the figure meant to illustrate it, and the flower sections are so sketchy (and even wrong as in *Pyrus malus*) that one fears for their influence on the students using the book.

In short, this is a book on promising lines, of general usefulness, but which might be much improved in later editions.

H. GODWIN

Stella Ross-Craig. *Drawings of British Plants.* With a foreword by Sir EDWARD SALISBURY. Part I: Ranunculaceae (44 plates), 96 pp., $9\frac{3}{4} \times 6$ in., 6s. net. Part II: Berberidaceae, Nymphaeaceae, Papaveraceae, Fumariaceae (22 plates), 56 pp., 1948. 4s. London: G. Bell and Sons, Ltd.

Miss Stella Ross-Craig has launched an enterprise which will have the good wishes of all botanists and naturalists interested in the British flora. Her project is to publish a series of some 1500–1800 black and white plates, each giving a series of illustrations of a single species of plant native to Britain, or, although alien, well established. From the plan at this initial stage are excluded microforms, critical species, varieties, casuals, and escapes from cultivation.

Publication takes the form of small separate parts, of which the first two are now available, the first containing 44 plates of members of the Ranunculaceae, and the second containing 22 plates of Berberidaceae, Nymphaeaceae, Papaveraceae and Fumariaceae.

Miss Ross-Craig, whose reputation as artist to the Kew Herbarium is already established, attains a remarkably high standard of line illustration. There is one habit drawing at natural size for each species, together with drawings of several appropriate botanical features, very generally including the underground parts, the fruit and the seed. The high degree of accuracy in representation will, indeed, make the drawings valuable scientific records, and the backing and advice of the Kew staff, supporting the artist's own botanical experience, sufficiently guarantee the identifications of the species illustrated. One supposes that only on points of merest detail of execution will Miss Ross-Craig's illustrations be found at fault, though doubtless there will be room to regret a few omissions, such, for instance, as *Papaver lecoqii*, from the British poppies.

Beneath the illustrations of each plate are the legends explaining them, together with a note on flower colour; it has no doubt been wise to omit any attempt to record primary diagnostic features, but many students and amateurs will regret this, and one cannot help feeling that the notes on flower colour will (mistakenly) be used in default.

In the long task of completion we trust that Miss Ross-Craig and her publishers will have the wide support their enterprise deserves.

Sir Edward Salisbury has contributed a justly commendatory foreword, in which many will note he decisively expresses his view that 'Whatever proportion of the flora of these islands may have survived the glacial epoch, no dispassionate assessment of the known facts can leave any doubt that it was a relatively small one', and adds truly enough 'The building-up of the British plant-population is never final'. We all recognize and deplore the meagreness of the facts on which to judge these matters, and works like this, by encouraging and maintaining critical interest in our flora, are the surest road to wider and safer knowledge.

H. GODWIN

Good, Ronald. *The Geography of the Flowering Plants.* Pp. 403, 71 line-drawings, 9 maps in colour, and 16 photogravure plates. 30*s.* net. 1947. Longmans, Green and Co.

Recent books on Plant Geography now make a substantial trilogy. To the *Historical Plant Geography* by E. V. Wulff, and *Foundations of Plant Geography* by Stanley S. Cain, is now added the work of Prof. R. D'O. Good of University College, Hull.

This latest publication adds much to our knowledge and will be essential to advanced study of phytogeography. It suffers from the unfortunate chance of having been finished just at the beginning of the war, and of having therefore undergone a delay of eight years in publication. This has had the natural effect that wherever work is referred to in a rapidly advancing field of inquiry (such as the application of cytogenetical ecological studies to evolutionary processes, or the bearings of pollen-analysis upon vegetational history) the picture strikes one as somewhat out-of-date. This is by no means true of the substantial sections of the book based upon Prof. Good's own researches, particularly the chapters upon the distribution of the genera and families of flowering plants, where a comprehensive collection and analysis of the facts has been long overdue. In this section of the book the frequent distribution maps are supplemented by very satisfactory line illustrations of unfamiliar genera.

Chapters of very particular interest to the British botanist are those on the History and Distribution of the British Flora, and on the Distribution of Plants within an English County. In the former the author takes a sensibly moderate position with regard to glacial extinction and nunatak survival. Not many of his colleagues will agree, however, that the difficulties of accounting for the Atlantic and Lusitanian species so characteristic of western Ireland have been overestimated. The first step in Prof. Good's argument is that 'The actual occurrence of these plants in south-west England and Ireland proves that their climatic and edaphic requirements are different from those of the generality of British plants only in so far as the conditions of south-west England and Ireland differ from those of the rest of the country. That is to say they are present within our boundaries because there are spots therein in which they can find a congenial home and the conditions they need.' But surely this begs the whole question: we invoke historical explanations of their present range precisely because we are *not* satisfied that they are limited solely by edaphic and climatic factors. The argument proceeds by stating that because the whole of Ireland was glaciated, immigration must have been post-glacial in date, and that 'the separation of Ireland from Britain clearly antedates the Pleistocene'. It now seems apparent that some of southern Ireland entirely escaped glaciation, and that large areas glaciated at one period escaped later glaciations. Moreover, the glacial eustatic lowering of sea-level by some hundreds of feet certainly reduced the significance of the Irish Sea as a barrier to plant spread. These facts do much to invalidate the final conclusion that 'hence the present Irish flora must have re-immigrated since (the Ice Age), and in doing so must have crossed the intervening sea. It is therefore clear that this sea has not proved a significant barrier to dispersal.'

The same comment of course applies here as to the argument 'Again, there is no reason to assume that the Straits of Dover have ever been wider than they are now, and hence they must always have been an even slighter obstacle to plant migration'. When we are seeking to use the facts of plant distribution to assess the dates and routes of migration, we are not entitled to begin from the premises that most of the flora must be reimmigrant, in order to explain that the subjects of more strikingly restricted range are also reimmigrant. There seems to be every reason to approach such questions as these by the identification

of subfossil remains of significant species from adequately dated levels in late-glacial and post-glacial deposits, a task already successfully begun by Jessen in Ireland.

In the 'Distribution of plants within an English County', Prof. Good describes the result of a phytogeographic survey of an area intermediate in size between those usually considered by phytogeographers on the one hand, and plant ecologists on the other. The county of Dorset was divided by the author into a grid of one mile squares, and over a period of years he worked out the distribution of flowering plants in the whole county. As Dorset offers a substantial range of topography and geology, and a lesser, but still considerable range of climate, the opportunity is provided of studying many instances of correlations of species distribution with the space distributions of these factors. Many phenomena of the greatest autecological interest are disclosed in this way, and indicate the possibility of more detailed and more experimental investigation. We may note, of very many, the case of *Primula vulgaris* increasingly prevalent with higher rainfall to the west, *Filipendula hexapetala* and *Verbascum nigrum* confined to the chalk at the north of the county and *Rumex crispus* and *Daucus carota* more frequent near the coast. Of great interest are the notes on recent changes in frequency; the diminution of *Adonis annua* and *Centaurea cyanus*, and the expansion of *Parentucellia* (*Bartsia*) *viscosa*.

The first part of the book concludes with a brief exposition of the significance of geological history and former distribution for phytogeographical study. Part II is devoted to the 'possible explanation' of phytogeographic facts set out in Part I in terms of the 'factors controlling plant distribution'.

A general review of the various hypotheses involved includes an account of Wegener's theory of Continental Drift (given the author's commendation as a possible means of resolving many problems of geographical distribution. There is also expounded the 'Theory of Tolerance', of which the most substantial point seems to be that the rate of adaptive modification of plant species is much less than the rate of plant migration. The Theory of Tolerance hardly seems to leave sufficient room to allow for many instances of absence (for instance in the British Isles) of species which grow well enough when introduced (as species of *Sarracenia*, *Rhododendron ponticum*, *Epilobium nummularifolium*, etc., in the British Isles) into native and natural plant communities. There seems no reason to doubt that it was the accident of plant dispersal at former times, rather than climate and soil during the present, that explains such facts. It is a more general criticism that the Theory of Tolerance is rather an outline of an approach to the problems of plant geography than a 'theory' which one expects to explain causative mechanism.

Short appendices and a long bibliography close the book. It is one for which we shall long be indebted to Prof. Good.

H. GODWIN

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BRITISH ECOLOGICAL SOCIETY

JOINT MEETING WITH THE BRITISH SOCIETY OF SOIL SCIENCE

HELD IN THE BOTANY DEPARTMENT, UNIVERSITY COLLEGE, LONDON, ON 28 APRIL 1948

'THE ORGANIC MATTER IN THE SOIL'

Prof. W. H. Pearsall opened the symposium with a paper entitled 'An Ecologist looks at the soil'. His approach was that of a practising ecologist, who must look at soils as materials for field study and particularly as highly dynamic systems. Prof. Pearsall discussed soils of British woodlands, taking his data from woods in the south of England, which have soils differing from those of woods in the north. The soil systems of natural woodlands function around three or four cycles, of which the most important is that following the annual leaf fall. The average annual accession of organic matter at leaf fall is from 1500 to 2000 g./sq.m. woodland surface. There is considerable difference in the chemical composition of the leaves of various tree species, and also in the ease with which they are attacked by living organisms.

Normally all this organic matter is broken down in the course of the year, giving no permanent accumulation. This represents a very high degree of activity and rate of breakdown, calculated as an average loss of 4–5 g. organic matter/sq.m. soil surface/day, which is equivalent to the liberation of 6–7 g. carbon dioxide/sq.m. soil surface/day.

It follows that a small reduction of activity will give an appreciable accumulation of organic matter. This can be brought about in three main ways—by leaching, by increase in soil acidity, and by changes in soil humidity. Data obtained by Clapham in Oxfordshire woodlands were cited to illustrate the changes of acidity in different types of soil throughout the year. The humidity of the soil alternates in southern England between a wetter and a drier period, the former lasting slightly longer than the latter. In the wetter period leaching is at a maximum, whilst in the drier period the soil is well aerated, leaching is at a minimum and oxidation at its maximum. In other parts of Britain where the high rainfall is sufficient to balance the evaporation, the soil is permanently damp with more or less anaerobic conditions resulting in very little oxidation and great accumulation of organic matter. This gives rise to the 'peat' of the soil chemist, but to the field ecologist it is the end-point of a series of increasing soil humidity with maximum disturbance of the annual cycle. The results of humus accumulation are, in fact, largely autocatalytic; once accumulation has begun it continues, because the water content of the soil which determines the continued accumulation is in itself determined by the humus content of the soil.

Mr W. R. C. Handley, in a paper entitled 'Mull-Mor as a dynamic equilibrium', reviewed the literature on a subject which has occupied the attention of ecologists and pedologists for a considerable time. He pointed out that many of the contradictions in the literature were due to the very different conditions under which different investigations

were made, and others to the looseness of definition. In his own paper he omitted soils subject to waterlogging, such as peat, in his consideration of mor, which was described as 'a mat of organic matter superimposed upon a mineral soil'.

He pointed out how difficult it was to define mull and mor in terms of single-value soil constants like organic matter, pH, base status, etc., and that there is no sharp line of demarcation between them. He referred to the work of Tamin and Fisher in regard to the mull-mor equilibrium and the importance of vegetation, and summed up by saying that the factor determining whether a mull or a mor is formed or maintained may be determined by the end-points of micro-organism activity, controlled primarily by the vegetation.

Dr J. L. Harley's contribution was entitled 'Soil organic matter and the distribution of soil flora', and as a basis for his discussion he took the fact that either mull or mor soils can develop under *Fagus*. The beech varies in form on the two types of habitat, especially in regard to the distribution of roots. There is a marked subsurface accumulation of roots in acid soils, decreasing on going to a mull. He showed how the micro-floral population in the soil varied in different habitats, and under the influence of different types of organic residues. He suggested that the distribution of roots may be the result of an upset in microbiological activity, and stressed the importance of both above-ground and subsurface accessions of organic matter.

The facile explanation that the concentration of beech roots is due to their seeking nutrients was dismissed as quite inadequate.

The development of a mor may be initiated by this subsurface concentration of roots forming a barrier to the mechanical mixing of litter in the soil by soil fauna. This may cause the litter to go through a relatively long period of decomposition before incorporation. In any case it is considered that further examination of micro-organismal activities in litter and humus layers of various natural soils, and the correlated distribution of roots and micro-organisms, will throw light on pedogenics.

Dr G. K. Fraser's paper on 'General trend of investigation of soil organic matter at the Macaulay Institute' was communicated by Dr Forsyth. At the Macaulay Institute the characteristics and composition of humus have been investigated chiefly from natural soils, as it is considered that such investigations are more fundamental than those relating to artificial types like arable soils and forest soils.

Little progress has been made in correlating soil quality with humus type by the use of 'proximate' analysis. Clearer correlations are obtained from studies of C/N ratios and by the rough determination of uronides.

Humus types have been recognized by simple colorimetric tests, confirming and extending the work of Springer, and by the use of neutral solvents such as fluorides and oxalates. The application of modern methods of chromatography in fractionating the alkali-soluble micro-colloidal organic matter has proved very useful.

It has been shown not only that different soils contain humic acids with different reactive groups, but that the molecule of humic acid from any one source varies. Purified humic acids appear to have a structure allied to lignin. A polysaccharide microbial product of wide occurrence and containing uronic groups appears to play a part in the formation of crumb structure in soils.

Wax-free organic matter appears to be made up of (1) a lignin-like polymer, (2) nitrogenous compounds (including one-third lignin-like and some nucleic acid), and (3) carbohydrates, present either as glucose uronic acid polymers and/or hexose-pentose groups.

Dr Crowther read a paper by **Mr J. M. Bremner** describing 'Recent work at Rothamsted on soil organic matter'. At Rothamsted for historical reasons work is largely carried out on agricultural soil, which of course does not receive the natural annual increment of organic matter as discussed by Pearsall. Recent work has progressed along two main lines: methods of extracting organic matter from the soil, and the study of nitrogen in the soil.

Interest in the development of appropriate methods for extracting organic matter from the soil resulted from the realization that the old-established use of caustic alkali probably decomposed and degraded the organic matter at the same time as extracting it. It has been shown by a systematic study of extractants that the organic matter is intimately associated with metals. Its solubility is determined in the main by the nature and extent of this association. The efficiency of a neutral salt extractant is apparently dependent upon the ability of its anion to remove interfering metals, of which calcium is one of the most important, either in the form of insoluble precipitates or as soluble co-ordination complexes. For efficient extraction the cation of a neutral salt extractant should be potassium, sodium or ammonium, as others cause precipitation of the organic matter. Of the many neutral extractants tested, sodium pyrophosphate was found to be the most efficient. Its use was recommended except where the primary purpose was the extraction of the largest possible amount of organic matter, when the old method of caustic alkali cannot yet be bettered.

In temperate regions only 1–2% of the nitrogen in the soil is inorganic, all the rest being organic. It has always been assumed with little real evidence that this is in the form of protein. The problem has been investigated by analysis of the products of hydrolysis of the organic nitrogen. Using the specific ninhydrin decarboxylation method it has been shown that at least one-third of the total nitrogen of the soils examined must be of a protein nature. This is a minimal fraction as some is destroyed during hydrolysis. Much of the remaining nitrogen in the soil is believed to be in the form of amino sugars, heterocylic nitrogenous compounds and nucleic acids.

Dr H. L. Riley gave the final paper in the series on 'An X-ray diffraction study of humification'. Humification is regarded as the first stage in the series of changes from vegetation to coal and to crystalline graphite.

As would be expected with such high molecular weight colloidal material, the composition of humic acid from peat and coal is not constant. Coals, peats and humus all give the same type of X-ray powder photograph, however, consisting usually of only two diffuse diffraction halves, the inner more intense than the outer. The diffraction broadening is due to the exceedingly minute dimensions of the colloidal diffracting units. It is customary to measure this broadening in terms of an hypothetical cylindrical crystallite of diameter a and height c.

A detailed study of the changes which occur in the diffraction broadening as coals and peats mature, and as coals and other substances are subjected to a stepwise carbonization, gives some insight into their ultimate crystallographic structure.

All organic matter with a high oxygen content shows a constant c dimension of the crystallite in carbonization. Peats behave in this way up to about 800° C., when the c dimensions rise sharply. In all, four classes of organic material can be recognized on the basis of behaviour of their a and c dimensions with changing temperature of carbonization. It is suggested that such information might have a bearing on the later stages of humification. For example, the degree of development of a benzenoid structure depends upon the proportion of carbon, and basicity might be influenced by carboxyl groups. The absorptive properties of humic materials are probably more important than chemical composition, and are probably governed by the original parent organic material. The author discussed other bearings that his results might have on the structure of humus and the process of humification, and concluded with the query as to whether it would not be easier, in studying humic acids, to study synthetic materials.

In the Discussion which followed the six papers many aspects of the subject were touched upon, including points not already mentioned in the papers.

The chairman, **Mr C. G. T. Morison**, asked whether there were such things as mull and mor, giving an example from Wales where the effect of altitude on soils, developed on the same parent material of old red sandstone, under the same type of woodland, was such that at 1000 ft. a typical mull is found, passing by gradual transition into a mor at 2000 ft.

Prof. Pearsall emphasized the importance of definition. The terms mull and mor represent extremes and must be used as the two end-points of a series, not as intermediate stages as is so often the case. A mull develops on a slightly acid or neutral soil, and supports an entirely different type of vegetation from a mor, which is all a mull is not—a hydrogen soil of black, greasy organic matter with no crumb structure, an absence of nitrates and earthworms, and a carbon dioxide liberation approximately one-quarter that of a mull.

Dr Day pointed out the importance of the relation between the physical and chemical nature of the soil and the vegetation. He also mentioned that the range round the equilibrium mull-mor must be remembered. His third point was a desire to know more about the subject of root layering.

Mr Swabey gave a short account illustrated by slides of some of the physical aspects of humus, in particular of the factors governing aggregation of soil into crumbs. He showed a slide of earthworms' casts from arable and grass land which had different structures, those from the grass land being less easily broken down than those from arable land. This was to be correlated with the different humic materials to be found in the two habitats.

Dr Watt pointed out that the data of the preceding papers had all been taken from soils where the balance with climate was unstable and the change mull-mor was easy. He emphasized that plants determine both the type of the humus and also the conditions under which it will be formed. Foresters are in a position to control both these. As an example of the part played by earthworms he referred to Lodge Wood in the Chilterns where a slight podsol is developed under the beech trees. In a gap formed by the death of a beech tree and colonized successively by *Deschampsia flexuosa*, birch and oak, the incipient podsol was being broken down, worms and moles were present, and the soil had become loose and friable.

Mr Elton called attention to the specific litter fauna found in some moist deciduous woods, and in flushes in them. The fauna is virtually aquatic, it skeletonizes the leaves and forms a specialized saprophytic community, for there are no green micro-organisms present. Another speaker mentioned the aquatic Hyphomycetes, described by Ingold, as a group of lower plants with a somewhat comparable habitat.

Other points raised included the differential palatability of litter for insects and earthworms; the toxic properties of litter, and in particular the presence of phenolic groups preventing the ready decomposition of pine sawdust; the possible effect of sun on humus formation; and the absence of useful information on the part played by roots in the humus cycle.

Prof. Pearsall summed up the results of the meeting by saying that whilst it was undoubtedly valuable for ecologists, agriculturalists, soil physicists and chemists to discuss common problems together, it must be emphasized that the ecologist is primarily interested in finding out what happens in the field, and the great danger of equating results obtained under different conditions, and by different approaches, must be realized.

J. Allison
R. L. Crocker

BRITISH ECOLOGICAL SOCIETY

SUMMER MEETING AT NEWCASTLE

5–9 July 1948

About thirty outside members enjoyed an extremely pleasant meeting at Newcastle. Men stayed at Henderson Hall and women at Easton Hall, and the Society is grateful to the University for making this very comfortable accommodation available.

The meeting opened at 8 p.m. on 5 July with a soirée in the Department of Botany at King's College, Newcastle, by kind permission of Prof. Meirion Thomas. About fifty members and guests were present. Refreshments were served and there were exhibits to explain and illustrate the forthcoming excursions. A very enjoyable evening ended soon after 10 p.m.

Tuesday, 6 July

The weather fortunately proving favourable the party travelled by motor-coach to Seahouses and at about 11 a.m. set out in small boats for the Farne Islands which lie between 1½ and 5 miles from the coast. They are in two groups separated by the mile-wide Staple Sound, and are composed of dolerite of the Whin Sill which forms cliffs round most of the islands. Their gently sloping tops are either of bare rock or covered with boulder clay upon which a peaty soil has developed. They are owned by the National Trust and kept as a sanctuary for the thousands of sea-birds which nest on them and for the grey seals which breed nowhere else along the east coast of Great Britain.

The first halt was made on Staple Island, the innermost of the outer group. From the landing point a short walk over slabs of slippery rock brought the party close to The Pinnacles, stacks up to 60 ft. high whose tops were thickly covered with guillemots while kittiwakes and shags were still nesting on the ledges of their almost vertical sides. Elsewhere, and especially by the ravine-like clefts which run inland from the coast, sea-birds were observed under ideal conditions. Members of the party ate their sandwiches within a few feet of nesting kittiwakes and shags, enjoying a close view of the different ways in which adult birds of the two species feed their nestlings. Lesser black-backed gulls hovered over the scene watching for unprotected youngsters, and puffins and guillemots constantly flew past. After lunch some attention was paid to the vegetation of the top of the island, notable especially for the luxuriant growth of *Silene maritima* (some plants with and some without anthocyanin pigmentation of their stems, leaves and sepals) and *Atriplex glabriuscula*, and for the curious peat-like cover, reaching a depth of 10–15 in. and apparently derived chiefly from the rhizomes and roots of *Puccinellia maritima* and *Silene maritima*. It was not clear why this accumulation should have taken place, since the peaty layer is certainly not waterlogged throughout the summer though it may be constantly wet with salt spray during winter. Other species of a scanty vegetation included *Cochlearia danica*, *Armeria maritima* and *Spergularia salina*. Before re-embarking the party spent a few minutes watching the numerous puffins at their nesting holes. No landing was made on the neighbouring island, Brownsman, but a great variety of birds could be seen on and near its cliffs.

The journey to Longstone, the outermost large island, brought the boats within sight of numbers of grey seals. The party then passed close to the ternery on Longstone where arctic and Sandwich terns were seen, and some members landed at the northern end of the island by the lighthouse made famous by Grace Darling. Returning along the west coast of the island a few roseate terns were identified and more seals were seen. Then the boats turned landwards and a last landing was made on the innermost island, Inner Farne. Here young arctic terns at various stages of development were watched on a strip of sandy shingle near the landing stage. The slopes above the ternery were covered with a lush vegetation in which *Urtica dioica*, *Rumex crispus* and *R. obtusiflorus*, *Cirsium arvense* and *C. vulgare*, *Conium maculatum*,

Holcus lanatus, Poa trivialis, Potentilla anserina, Myosotis arvensis and *Ranunculus repens* were conspicuous constituents. The path up this slope led to a group of disused buildings including a church and a tower. In the walled enclosure, formerly a vegetable garden and chicken run, were *Senecio jacobaea, Stellaria media, Silene maritima, Plantago coronopus* and two patches of *Amsinckia* sp., the last presumably introduced in chicken food. Above the buildings a rabbit-nibbled turf was found to contain dwarf forms of *Sagina procumbens* and *Cerastium tetrandrum*, while a brackish pool nearby yielded *Ranunculus baudotii*. Nesting eiders were seen in longer grass towards the south, and some members of the party watched fulmars which now nest on this island. Tea was later provided at Seahouses and the party returned to Newcastle after a most delightful day during which all the botanists became enthusiastic bird-watchers.

Wednesday, 7 July

The next day the party went, again by motor-coach, to Durham and then on to Butterby Marsh, about 2 miles south of the city by the River Wear. The marsh occupies the bed of an old loop of the river at a point where the valley widens. In order to reduce the frequency of floods in this part of the valley a channel was cut across the neck of the loop in 1811, and later an embankment finally cut the loop from communication with the main river channel. The total area is about sixteen acres, of which the greater part is marsh, there being only about three acres of open water remaining. Water is supplied now by small inflow channels which run only in winter. The pH of the water is 6·5-7 and the floor is a thick black mud from which bubbles of hydrogen sulphide arise on disturbance. A species-poor phytoplankton consisting only of species of *Mallomonas, Dinobryon, Chlamydomonas, Eudorina, Peridinium* and *Fragilaria* is present in winter, following the resumption of inflow and the onset of decay of the macrophytic vegetation. The vegetation was described in this *Journal* by Dr B. Millard Griffiths (*J. Ecol.* **20**, 105–27), and his account still gives an excellent picture of the area. There have been certain changes, notably in the further diminution of the area of open water and a considerable reduction in the abundance of *Rumex hydrolapathum*. Dr Valentine pointed out to the party that this dock is not a common plant in the north, and on the European mainland it extends northwards only to South Sweden and the neighbourhood of Oslo. He thinks it likely that the changes at Butterby Marsh may be related to hard frosts when the water level was low during the recent severe winter.

A walk along the east bank of the Long Pool showed the main characteristics of the marsh vegetation. Within an outermost belt of *Nuphar lutea* there follow reed-swamp communities dominated locally by *Equisetum limosum* (going furthest into the water), *Sparganium ramosum, Iris pseudoacorus, Phalaris arundinacea* and *Rumex hydrolapathum*. *Oenanthe phellandrium* and *Glyceria fluitans* are locally prominent in the reed-swamp. Next follows a community in which *Phalaris arundinacea* is the chief constituent but with many associated species, especially on the landward side, including *Caltha palustris, Myosotis palustris, Alisma plantago-aquatica, Stellaria alsine, Valeriana officinalis, Lycopus europaeus, Galium palustre* subsp. *elongatum, Mentha aquatica*, etc., and then, further landward, a zone with *Juncus inflexus* dominant and much *Filipendula ulmaria, Senecio aquatica, Achillea ptarmica, Juncus effusus* and *Polygonum amphibium*.

The Typha Marsh farther north lies in a shallow basin and is dominated throughout its centre by *Typha latifolia*. Surrounding the Typhetum to the east is a narrow belt of *Sparganium ramosum* and then one of *Iris pseudoacorus* and *Juncus effusus*, with occasional plants of × *J. diffusus*. Finally, between this and the firm pasture, there is a strip dominated by *J. inflexus*. To the west of the Typhetum there is a strip of open water. *Salix fragilis* is thinly scattered through the area and forms a close fringe on the two sides of the western strip of open water.

Later stages in a succession towards fen woodland are seen at the northern end of the loop where, in very wet peat, *Salix atrocinerea, S. fragilis* and *Alnus glutinosa* form a partially closed canopy over a community dominated by *Iris* and *Equisetum limosum* with occasional residual *Typha*. Throughout this region *Rumex hydrolapathum* has diminished greatly in abundance.

During the walk back to the coaches a male-sterile plant of *Silene cucubalus*, with flowers less than 1·5 cm. in diameter, and some patches of *Doronicum pardalianches* were noticed.

Later the party was conducted by Dr Valentine to see grassland on Magnesian Limestone near Cassop

and Quarrington. The vegetation was typical of the northern lowland facies of limestone grassland, the presence of *Sesleria coerulea* being a feature of interest.

On returning to Durham the party had tea in the Departments of Botany and Zoology at the Durham Colleges Sciences Laboratory and was then conveyed to the centre of the city. Many features of great architectural and historic interest were seen in the course of a conducted tour of the magnificent Norman cathedral, and the guide was suitably thanked by Dr Varley for placing his time and his intimate knowledge of the Cathedral and its history at our disposal. Dinner followed in the dignified atmosphere of the Hall of Durham Castle, by generous permission of the Master of University College, to whom, and to other members of the University who had contributed so much to the Society's enjoyment and instruction, the Vice-President, Mr V. S. Summerhayes, expressed the Society's thanks. The party then returned to Newcastle at about 10 p.m.

Thursday, 8 July

On Thursday an early start by motor-coach enabled us to reach the High Force Hotel, Upper Teesdale, by about 11.30 a.m. At a point a half mile or so up the valley the party left the coaches and took the path to Cronkley Scar. There was a short halt while Prof. Wager, of Durham University, gave a lucid description of the geological features of the area. He pointed out the geomorphological significance of the intrusive Whin Sill which forms here a massive horizontal sheet through which the Tees has cut a steep-sided valley, Cronkley Scar being its northern side. The Sill has caused metamorphosis of the Carboniferous Limestone in its close vicinity to produce the well-known Sugar Limestone, upon which so many curiously localized plant species are found. During the last advance of the ice a glacier filled the Tees valley, but apparently did not cover the tops of the higher surrounding hills. Drumlins now occupy the valley floor at this point.

The path took the party across the Tees and through the floristically rich meadows of the valley floor. From a long list of interesting species mention may be made of the richly coloured northern orchid, *Orchis purpurella*, which was found in two slightly differing colour forms, *O. fuchsii* and *O. ericetorum*, *Trollius europaeus* still in flower, *Viola lutea* in its full colour range, *Cochlearia alpina* and *Rhinanthus stenophyllus*. On the north side of the valley the path climbed a Whin Sill slope with juniper scrub and a good deal of *Digitalis*, and then joined the old sheep track to Cronkley Fell. On the way up the face of the escarpment several ring ouzels were seen on *Pteridium-Calluna* ground. Lunch was eaten in a sheltered spot near the top, and then the party examined the striking vegetation of the Sugar Limestone. The more strictly localized species fall into two groups: those of loose dry limestone and those of stream-beds and flushes. Amongst the former are *Helianthemum canum*, *Dryas octopetala*, *Minuartia verna*, *Polygala oxyptera* and *P. amara*, *Galium pumilum* and *G. boreale*, *Gentiana verna*, *Polygonum viviparum* and *Carex capillaris*; amongst the latter *Thalictrum alpinum*, *Primula farinosa*, *Tofieldia pusilla*, *Juncus alpinus* and *J. triglumis*, of which the last may perhaps have been planted early last century. Zoologists found much to interest them in the fauna of the Tees and of smaller streams. The party returned to the High Force Hotel for tea and then drove back to Newcastle.

Friday, 9 July

On the last morning the coaches conveyed the party first to the Dove Marine Laboratory at Cullercoats. The Acting Director explained that the Laboratory began as a wooden hut where research was conducted for the Northumbrian Fisheries: the present building was erected in 1904. The Laboratory is now a part of King's College, Newcastle, and Prof. Hobson of that College is its Director. But it also conducts Fisheries Research for the Ministry of Agriculture and Fisheries, is a Public Aquarium and sells zoological specimens to schools and University departments. The party spent the remainder of the morning in examining the large collection of living animals kept in the laboratory, and, armed with jars, in some shore-collecting under rather unfavourable weather conditions. The Staff of the Laboratory kindly gave a great deal of their time in demonstrating the Aquarium, and members of the Society were much interested in the trial-and-error technique whereby the species-composition of viable mixed communities is determined. Combinations of lobster and coal-fish, of gurnard and octopus, and of whiting and edible crab had been found satisfactory as judged by the survival of the weaker partner. The body-movements and colour

changes of the octopus were shown to a fascinated audience, and admiration was expressed at the beauty of the collection of sea-anemones. In another room of the building the large collection of living crabs, lobsters, prawns, echinoderms and molluscs were inspected with interest.

After a sandwich lunch in the Laboratory the party moved by coach to the sand-dunes at Seaton Sluice. These proved of very great ecological interest, especially to botanists familiar only with more southerly dune areas. The area is dominated for the most part by *Ammophila arenaria*, with *Carex arenaria* and *Festuca rubra* playing much the same roles as farther south. But the yellow dune stages are characterized by the abundance of three striking species: *Thalictrum arenarium*, *Geranium sanguineum* and *Astragalus danicus*, all of which were in full flower. The ruby-red *Orchis latifolia* subsp. *coccinea* was found in damp hollows, and the discovery of *O. praetermissa* surprised many members, since this species has not been reported so far north. The presence of free calcium carbonate in the sand was suggested by the occurrence of *Viola hirta*, *Anthyllis vulneraria*, *Cerastium arvense*, and *Leontodon hispidus* as well as *Geranium sanguineum* and *Astragalus danicus*. In damp lows between the dune ridges *Juncus inflexus*, *J. conglomeratus*, *J. articulatus* and *J. gerardi*, *Carex nigra*, *Agrostis stolonifera*, *Filipendula ulmaria*, and *Lathyrus pratensis* were conspicuous.

An early return to Newcastle enabled some members to catch trains that evening, others leaving on the following day after a highly successful meeting up to the best pre-war standards. Dr Varley and Dr Valentine and all the others who helped with the excellent arrangements are much to be thanked.

BRITISH ECOLOGICAL SOCIETY

REVENUE ACCOUNT FOR THE YEAR ENDING 31 DECEMBER 1947

Income

	£	s.	d.	£	s.	d.
Subscriptions received, including arrears, and *less* Payments in advance						
Members taking *Journal of Ecology* only	323	14	0			
Members taking *Journal of Animal Ecology* only	201	5	6			
Members taking both Journals	194	10	0			
Associates	1	2	6			
	720	12	0			
Add Reserve brought forward from 1946 for *Journal of Ecology*, vol. 34	304	0	0			
				1024	12	0
Interest on Investments	72	0	0			
Interest on Deposit Account	2	11	7			
Interest on P.O. Savings Bank Account	24	0	0			
				98	11	7
Index to *Journal of Ecology*, vols. 1–20, Sales, less Cost				6	14	10
				£1129	**18**	**5**

Journal of Ecology, vols. 34 and 35	£	s.	d.	£	s.	d.
Sales: Current volume 34	663	11	6			
Current volume 35	551	13	2			
Back volumes and parts	643	0	10			
Reprints of papers	50	8	2			
Advertising		18	11			
	1909	12	7			
Balance (see above, under Expenditure)	28	8	0			
				£1938	**0**	**7**

Journal of Animal Ecology:	£	s.	d.	£	s.	d.
Sales: Current volume 16	451	7	8			
Back volumes and parts	259	8	6			
Reprints of papers	59	1	0			
Grant	1	0	0			
	770	17	2			
Balance (see above, under Expenditure)	83	12	3			
				£854	**9**	**5**

Expenditure

	£	s.	d.	£	s.	d.
Working Expenses:						
Travelling	15	15	7			
Postages	11	15	6			
Clerical assistance	10	0	0			
Meeting expenses	6	15	10			
Printing and Stationery	6	15	9			
Audit Fee	6	6	0			
Memorandum on Wild Life Conservation	4	14	2			
Typing and duplicating	1	13	2			
Bank charges	1	10	8			
				64	7	3
Grant to Freshwater Biological Association				10	0	0
Life Membership Subscription to Yorkshire Naturalists Trust				10	0	0
Subscription to Parliamentary and Scientific Committee				10	10	0
Journal of Ecology. Cost *less* Sales				28	8	0
Biological Flora of British Isles:						
Cost of Printing, Commissions, etc.	246	15	8			
Less sales of Reprints, etc.	67	14	1			
				179	1	7
Journal of Animal Ecology. Cost *less* Sales				83	12	3
Balance—Surplus for the Year (To Balance Sheet)				385	19	1
				743	19	4
				£1129	**18**	**5**

Journal of Ecology, vols. 34 and 35	£	s.	d.	£	s.	d.
Cost: Volume 34, Paper, Blocks, Printing and Binding				940	7	5
Volume 35, Paper, Blocks, Printing and Binding				675	17	4
Publishers' Commission				255	18	10
Carriage, etc.				49	2	8
Insurance of Stock				6	11	0
Cost of Copies bought in				9	10	0
Sundry Expenses					13	4
				£1938	**0**	**7**

Journal of Animal Ecology:	£	s.	d.	£	s.	d.
Cost: Paper, Blocks, Printing and Binding				713	15	8
Publishers' Commission				98	4	7
Carriage				20	15	5
Insurance of Stock				11	13	9
Fee for checking references				10	0	0
				£854	**9**	**5**

BALANCE SHEET AT 31 DECEMBER 1947

Assets

	£ s. d.	£ s. d.
Cash in hand at Westminster Bank		
Current Account	249 17 7	
Deposit Account	850 0 0	
		1099 17 7
Post Office Savings Bank Account ...		1034 8 4
Publishing Account due from the Cambridge University Press:		
Journal of Ecology	627 4 6	
Journal of Animal Ecology ...	408 0 1	
Biological Flora of the British Isles ...	27 16 9	
		1063 1 4
Investments at Cost:		
£1200 of 3½% War Loan Stock ...	1230 4 1	
£700 of 3% Savings Bonds 1960/70 ...	700 0 0	
£300 of 3% Savings Bonds 1965/75 ...	300 0 0	
		2230 4 1
		£5427 11 4

A further Asset, not valued, is the Unsold Stock of Journals, Index Volume and *Biological Flora* Reprints held by the Publishers for the Society.

VICTOR S. SUMMERHAYES
ALEX. S. WATT
Hon. Treasurers.

Liabilities

	£ s. d.	£ s. d.
Members' Subscriptions, prepaid for 1948 ...	12 0 6	
Library Fund	1 5 0	
Printing Accounts due to the Cambridge University Press:		
Journal of Ecology, Vol. 34 (2 Accounts) ...	212 2 3	
Journal of Ecology, Vol. 35 (2 Accounts) ...	618 5 11	
Journal of Animal Ecology, Vol. 16, No. 2 ...	369 5 10	
Biological Flora of the British Isles (3 Accounts) ...	98 2 0	
Expenses due to H. Godwin	1 18 0	
		1299 14 0
General Revenue Account—Surplus in hand:		
Balance at 31 December 1946	3370 12 6	
Surplus for the year 1947	743 19 4	
		4114 11 10
		£5427 11 4

Audited and found correct, and as shown by the Account Books of the Society. The Bank Balance has been verified by Bank Certificate, and also the Investments.

120 BISHOPGATE, E.C. 2
and
231a HIGH ROAD, LOUGHTON, ESSEX
16 *August* 1948

WM NORMAN & SONS
Chartered Accountants

BIOLOGICAL FLORA OF THE BRITISH ISLES

URTICA L.

P. GREIG-SMITH

URTICACEAE (UREREAE). A widespread genus of annual or perennial, monoecious or dioecious herbs, with about 40 species. Leaves opposite with free, occasionally connate, lateral stipules. Flowers in axillary panicles or racemes. Male flowers: perianth 4-partite, segments equal, stamens 4, inflexed in bud, deflexing explosively when the pollen is ripe; rudimentary ovary generally present. Female flowers: perianth 4-partite, 2 outer segments smaller than the inner; ovary ovoid with a sessile brushlike stigma, containing a single erect basal orthotropous ovule. Fruit an achene with persistent perianth.

Six species have been recorded from Britain, representing both the sections into which Weddell (1856) divides the genus:

1. Inflorescence androgynous
   A. Stipules free
      a Petiole short **U. urens** L., **U. flabellata** H. B. & K.
      (*b* Petiole long)
   (B. Stipules united)
2. Inflorescence unisexual
   A. Stipules free
      a Inflorescence spherical **U. pilulifera** L.
      b Inflorescence a spike or panicle **U. dioica** L., **U. gracilis** Ait., **U. incisa** Poir.
   (B. Stipules united, apices sometimes bifid)

(This summary of Weddell's classification is copied from Fothergill (1936). The latter supports this arrangement on the basis of chromosome structure.)

U. dioica is native. *U. urens*, though almost always associated with man, is almost certainly native. *U. flabellata*, a native of Ecuador, has been reported from Bradford (*Rep. Bot. Exch. Club*, **6**, 622, 1923). *U. pilulifera*, probably originally introduced, was long known from restricted localities in East Anglia but is now probably extinct there. It has occurred sporadically elsewhere in England and Ireland. *U. gracilis* (? var. *lyalii* Grey), a North American species, closely related to *U. dioica*, has been reported from Frizinghall, Yorkshire (Lees, 1941). Selander (1947) has shown that *U. dioica* var. *sondenii* Simm of northern Scandinavia is closer to *U. gracilis* than to *U. dioica*. He suggests the reduction of *U. gracilis* to subspecific rank as *U. dioica* subsp. *gracilis* (Ait.) Selander with the subspecies in North America and var. *sondenii* (Simm) Selander in Europe. *U. incisa*, native of Australia and New Zealand, has been reported from Devon (*Rep. Bot. Exch. Club*, **6**, 622, 1923). *U. hispida* DC., generally considered a variety of *U. dioica*, is recorded doubtfully by Druce (1928).

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Fothergill, P. G. (**1936**). Somatic chromosomes in *Urtica. Proc. Univ. Durham Phil. Soc.* **9**, 205.
Lees, F. A. (**1941**). *A Supplement to the Yorkshire Floras.* Ed. Cheetham, C. A. and Sledge, W. A. London.
Selander, S. (**1947**). *Urtica gracilis* Ait. in Fennoscandia. *Svensk bot. Tidskr.* **41**, 264.
Weddell, H. A. (**1856**). Monographie de la famille des Urticées. *Arch. Mus. Hist. nat. Paris*, **9**.

FOSSIL RECORDS OF *URTICA*

(From information supplied by Miss A. P. CONOLLY)

U. urens

Clactonian (*Early Palaeolithic*). Warrener, Reid & Chandler (1923) list 'cf. *U. urens* ident. Clement Reid' from the *Elephas antiquus* beds of Clacton-on-Sea.

Early Iron Age. Lidbury Camp, Wilts. (Cunnington, 1917).

U. dioica

Middle Pliocene. Castle Eden, Co. Durham (Reid, 1920). Interglacial loess of the Durham coast (Trechmann, 1919). List includes '*U. dioica* var. ?'. The date is given as older Middle Pliocene, but certain recent authors suggest a much more recent date for these deposits.

Clactonian (*Early Palaeolithic*). *Elephas antiquus* beds of Clacton-on-Sea. Warrener, Reid & Chandler (1923) list *U. dioica* in beds M, L, Q, W, Y, YY and Z, of which N to Z are the Elephant beds.

Bronze Age. Minnis Bay, Kent (Conolly, 1941).

Zone VIII of Jessen's Irish Quaternary succession. Lacustrine beds near Dunshaughlin, Co. Meath, det. Knud Jessen (Mitchell, 1940).

Urtica sp.

Early Iron Age. Glastonbury (Bulleid & Gray, 1911–17).

REFERENCES

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Conolly, A. P. (1941). Data for the study of post-glacial history. VII. A report of plant remains from Minnis Bay, Kent. *New Phytol.* **40**, 299.

Cunnington, M. E. (1917). Lidbury Camp. *Wilts. Archaeol. Nat. Hist. Mag.* **40**, 23.

Mitchell, G. F. (1940). Studies in Irish quaternary deposits: some lacustrine deposits near Dunshaughlin, County Meath. *Proc. R. Irish Acad.* **46 B**, 13.

Reid, E. M. (1920). On two preglacial floras from Castle Eden, County Durham. *Quart. J. Geol. Soc.* **76**, 104.

Trechmann, C. T. (1919). On a deposit of interglacial loess and some transported preglacial clays on the Durham coast. With a preliminary description of the plant remains by E. M. Reid. *Quart. J. Geol. Soc.* **75**, 173.

Warrener, S. H. (1923). The *Elephas antiquus* bed of Clacton-on-Sea (Essex) and its fauna and flora. With Appendix I: The fossil flora of Clacton-on-Sea by **E. M. Reid** and **M. E. J. Chandler.** *Quart. J. Geol. Soc.* **79**, 606.

INSECTS AND FUNGI ASSOCIATED WITH *URTICA*

INSECTS (O. W. RICHARDS)

Urtica is a food of a great variety of insects, but the following list includes only species in which the association is regular. Most records do not specify the species of *Urtica*, but are likely to intend *U. dioica*. Where there is a definite record for *U. urens* the name of the insect is followed by the letter *u*. The British distribution of the insects is given when it is sufficiently known.

THYSANOPTERA

Thrips urticae Fab., breeds on *Urtica*, perhaps confined to it. The flowers are visited by *Taeniothrips atratus* (Hal.), *T. vulgatissimus* (Hal.), *T. picipes* (Zett.) and *Thrips tabaci* Lind.

HEMIPTERA-HOMOPTERA

APHIDIDAE: *Macrosiphum carnosum* (Buckt.) (*M. urticae* Schrank) v.c. and widespread. *Aphis urticaria* Kalt., *u.*, c. on *Urtica* on stem and leaves, often curling the latter into a dense tuft, widespread. *Pergandeida stanilandi* Laing, Middx. and Lancs.

PSYLLIDAE: *Trioza urticae* (L.), *u.*, c., deforming the leaves, widespread.

TYPHLOCYBIDAE: *Eupteryx urticae* (Fab.), *E. aurata* (L.), *E. cyclops* Mats. (*E. britteni* Edw.), *E. stachydearum* (Hardy), *E. collina* Flor, *E. vittata* (L.), *E. atropunctata* (Göze). The above seven species are all more or less common on *Urtica* but are also found on *Labiatae*, the first three less often so. The species are probably widespread.

EUSCELIDAE: *Cicadula variata* (Fall.), said to be attached to *Urtica*, England.

BYTHOSCOPIDAE: *Macropsis tibialis* (Scott), (Edwards, 1908).

HEMIPTERA-HETEROPTERA

LYGAEIDAE: *Heterogaster urticae* (Fab.), occ. in southern England and Ireland. *Scolopostethus thomsoni* Reut. and *S. affinis* (Schill.), both c. on *Urtica* and widespread.

CAPSIDAE: *Phytocoris ulmi* (L.), widespread and c., possibly predacious. *Calocoris sexguttatus* (Fab.) and *C. norvegicus* (Gmel.), both widespread and c. on *Urtica*, though often found on other plants. *Lygus pabulinus* (L.), *L. lucorum* (Meyer-Dür) and *L. kalmi* (L.) are widespread and especially c. on *Urtica*. *Liocoris tripustulatus* (Fab.), c. and almost confined to *Urtica*; will feed on Aphides (Goddard, 1935). *Dicyphus errans* (Wolff), chiefly on *Urtica*, widespread. *Orthonotus rufifrons* (Fall.), chiefly on *Urtica*, southern England and Wales. *Plagiognathus arbustorum* (Fab.), widespread and especially c. on *Urtica*; will feed on Aphides (Goddard, 1935).

COLEOPTERA

NITULIDAE: *Brachypterus urticae* (Fab.) and *B. glaber* (Steph.), c. and widespread on flowers in which larvae develop.

CHRYSOMELIDAE: *Crepidodera ferruginea* (Scop.), adult widespread, c. on *Urtica*.

CURCULIONIDAE: *Apion urticarium* (Herbst), *u.*, larvae in stem, v. local in southern England. *Phyllobius urticae* Deg., adult c. on leaves, larvae possibly on roots, widespread. *Ceuthorrhynchus pollinarius* (Forst.), c. and widespread. *C. quadrimaculatus* (L.), *u.*, c. and widespread, adults on leaves, larvae probably in stems.

DIPTERA

CECIDOMYIIDAE: *Dasyneura urticae* (Perris), *u.*, larvae in subspherical swellings, usually near base of leaf, occasionally on flower stalks, c. and probably widespread. Bagnall & Harrison (1921, p. 152) record *Clinodiplosis urticae* Kieff. as a commensal in the galls of the preceding.

AGROMYZIDAE: *Agromyza reptans* Fall., *u.* (also on *Parietaria*), larva in mine which first proceeds along edge of leaf, later widening to blotch more on lamina, c., at least in southern England. *A. anthracina* Meig. (also on *Parietaria*), larva in mine which starts on lamina and is very contorted, later becoming a blotch, species probably British. *Melanagromyza aeneiventris* (Fall.) and *Phytomyza lateralis* Fall., both breed in stems especially of *Compositae*, but also of *Urtica*. *Phytomyza flavicornis* Fall., larvae in stems.

LEPIDOPTERA

NOCTUIDAE HYPENINAE: *Hypena proboscidalis* (L.), larvae feed on leaves, c. and widespread.

NYMPHALIDAE: *Aglais urticae* (L.), larvae feeding gregariously on leaves, ab. and widespread. *Nymphalis io* (L.), larvae feeding gregariously on leaves, c. and widespread, except in extreme north. *Vanessa atalanta* (L.), larvae solitary on leaves (more rarely on *Parietaria* and *Humulus*), c. and widespread.

PYRAUSTIDAE: *Notarcha ruralis* (Scop.), larva in spun leaves, c. and widespread, except in extreme north. *Eurrhypara urticata* (L.), larva in spun leaves (also of certain *Labiatae*), c., England to Yorkshire, Ireland.

GLYPHIPTERYGIDAE: *Simaethis fabriciana* (L.), larva in web on dorsal side of leaf (also of *Parietaria*), ab. and widespread.

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Also: **Butler,** *Hem.-Het.;* **Edwards,** *Hem.-Hom.;* **Fowler,** *Coleopt.* **3, 4, 5; Hendel,** Lief. **52, 54, 56, 58, 66, 85, 90, 92, 94, 96; Meyrick,** *Lepidopt.;* **Theobald,** *Aphid.* **1, 2, 3.**

NEMATODES (A. SMITH)

Heterodera schachtii Schmidt has been reported on *Urtica dioica* in this country, and this species, together with *Appelenchoides ritzema-bosi* Schwartz, on *Urtica urens* (*Nemat. Cat.*).

FUNGI (A. SMITH)

The host references to fungi on *Urtica* in the British Isles are in a very unsatisfactory state—practically all referring to 'nettle' or '*Urtica* sp.'. It should be noted that *U. urens* practically disappears at the first frost and offers no subsistence for saprophytes; practically all records probably in fact refer to *U. dioica*. No fungi appear to have been recorded in the British Isles on *U. pilulifera*.

Unless noted to the contrary the records are for '*Urtica* sp.' or 'nettle'.

PHYCOMYCETES

PERONOSPORALES: *Pseudoperonospora urticae* (Lib.) Salm. & Ware on *Urtica dioica* and *U. urens. Peronospora debaryi* Salm. & Ware on *Urtica urens.*

ASCOMYCETES

ERYSIPHALES: *Erysiphe polygoni* DC. usually on *Urtica dioica.*

SPHAERIALES: *Aporhytisma urticae* (Fr.) vön Hohn. on *Urtica dioica. Diaporthe tulasnei* Nits., *Didymella superflua* Sacc., *Leptosphaeria acuta* (Hoff. ex Fries) Karst., *Ophiobolus erythrosporus* (Riess) Wint., *O. ulnasporus* (Cooke) Sacc., *O. immersus* Traill, *Lophiotrema sex-nucleatum* Sacc.

HELOTIALES: *Cyathicula infexa* Sacc., *Helotium herbarum* Fr., *Mollisia urticola* Phill., *Phialea urticae* Sacc., *Trichopeziza leucophaea* Rehm., *T. plano-umbilicata* Sacc., *T. sulphurea* Fuck.

BASIDIOMYCETES

UREDINALES: *Puccinia caricis* (Schum.) Rebent., aecidial stage. Other stages on *Carex* spp. This is usually on *Urtica dioica* but was found in 1943 by E. A. Ellis on *U. urens*, which in normal seasons is not sufficiently advanced in growth when teleutospores germinate. *Uromyces urticae* Cooke appears to have no foundation in fact.

FUNGI IMPERFECTI

COELOMYCETES: *Phyllosticta urticae* Sacc. on *Urtica dioica. Phoma acuta* Fuck. on *Urtica dioica. Phoma urticae* Sch. & Sacc. on *Urtica dioica. Ascochyta urticae* A.L.Sm. & Ramsb. on *Urtica dioica. Septoria urticae* Rob. & Desm. on *Urtica dioica* and *U. urens*.

MONILIALES: *Cylindrocolla urticae* (Pers. ex Fries), *Acrotheca acuta* Grove, *Hormiscum laxum* Wallr., *Acrothecium simplex* B. & Br., *A. simplex* var. *elatum* Grove, *Brachycladium penicillatum* Corda, *Ramularia urticae* Ces. in Rab.

A minor ecological role might be ascribed to *Puccinia caricis*, but any crippling effect is confined to early growth, and even then it is only present in quantity in close proximity to sedges. *Ramularia urticae* is of even less importance.

REFERENCES

List Pyrenomyc.; Br. Rust F.; Br. Stem and Leaf F. **1, 2**; **Oudemans**, *Enum.* **2**; **Sacc.** *Syll.; List Hyphomyc.*

Lond. Cat. (Ed. 11) No. **1730**

Urtica dioica L.

P. GREIG-SMITH

A perennial herb with an extensive sympodial system of rhizomes and stolons, rooting at the nodes and turning up to form the aerial shoots. Shoots generally unbranched, but occasionally showing some branching at the top, especially in the autumn. (Branching is usually a result of injury to the apex. See V (c) below.) Leaves opposite, petiolate, lower ovate more or less cordate, upper more or less lanceolate, coarsely serrate, under dry, sunny conditions sometimes small and divided almost to the midrib. Stipules free, lanceolate, entire, somewhat membranous, caducous. Dioecious, inflorescences axillary, four per node, varying from a loosely branched to a compact, spike-like panicle. Achenes small (*c.* 1 × 0·75 mm.). Stem and leaves more or less densely covered with hairs and stinging hairs. Stinging hairs absent from the inflorescence and occasionally (var. *subinermis* Uechtritz) almost lacking except at the base of the stem.

Very variable in size, leaf and inflorescence form, and degree of hairiness. A large number of varieties have been described (see Aschers. & Graebn. **4**, etc.). Occasional male and hermaphrodite flowers occur on female plants, and occasional female and hermaphrodite flowers on male plants. A monoecious variety has been described from Europe. According to Druce (1928) the following varieties occur in Britain. Their taxonomic status is uncertain: *angustifolia* Wimm. & Grab.; *atrovirens* Gren. & Godr.; *holosericea* Fries; *horrida* Rouy; *incisa* Dr.; *microphylla* Hausm.; *purpurascens* (Dr.); *rotundata* (Dr.); *subinermis* Uechtr.

Urtica dioica *L.*

A species found throughout the British Isles in widely varying habitats. Found on most soil types, except possibly acid peat. Native probably only in fen carr and possibly in pedunculate oakwood. Elsewhere a follower of man.

I. *Geographical and altitudinal distribution.* Recorded from all British and Irish vice-counties. Abundant wherever there is much disturbed ground.

Probably native in Europe and Russian Asia from the Mediterranean to the arctic regions, and adventive in India, Tibet, China, Australia, New Zealand, North and South Africa, and North and South America. Absent from the tropics.

Fig. 1. *Urtica dioica* L. Vice-comital distribution in the British Isles and (inset) distribution in Europe.

Mainly a lowland species, the limits corresponding broadly with those of habitation. At higher altitudes always closely associated with man or his animals. Ascends to 2440 ft. (744 m.) at Knock Ore Gill, where 'probably introduced by sheep' (Wilson, 1938), and Milburn Common (*Alt. range Br. Pl.*), 2400 ft. (731 m.) on Mickle Fell (Baker, 1906), 2250 ft. (686 m.) on Highfield (Baker & Tait, 1868), 2030 ft. (619 m.) in west Lancashire (Wheldon & Wilson, 1907), 1810 ft. (552 m.) on Tal-y-Fan (*Alt. range Br. Pl.*), 2750 ft. (838 m.) on Breadalbane Hills (White, 1898), 2200 ft. (670 m.) on Mangerton (Scully, 1916) and 1200 ft. (366 m.) on Ben Bulben range (Praeger, 1909). In Europe

ascends to 8578 ft. (2615 m.) on Arose Weisshorn (Braun-Blanquet & Rübel, 1933), 8112 ft. (2472 m.) at Great St Bernard Hospice (Hegi, *Fl.* 3) and 7907 ft. (2410 m.) in Valais (Aschers. & Graebn. 4). In Tibet it is found at 8000–10,000 ft. (2439–3048 m.) (sp. in Herb. Univ. Camb.).

II. *Habitat.* In natural habitats almost confined to woodland, especially fen carr and pedunculate oakwood. In the former it is probably native, but in oakwood it is often associated with the sites of former habitations, e.g. in Buff Wood, Cambs, it is confined to a part of the wood where pieces of thirteenth-century pottery have been found (Dr A. S. Watt). Horwood & Noel (1933) and White (1912) note its association with earthworks. Occasionally found in shingle bays above high-tide mark, e.g. north side of Loch Sunart (R. H. Richens). Oliver (1912) states that it colonizes at the foot of bare shingle banks on beaches of the 'apposition type' near Rye 'in the neighbourhood of habitations and traffic' and slowly spreads up to the summit, being followed by a closed community of fine grasses which eventually suppress it.

Elsewhere it is an almost universal follower of man, occurring on heaps of wood, metal, stones (rooted in the underlying soil), earth and sand, along the foot of walls, around sheep and cattle folds and at the foot of stacks. Once established in such habitats it frequently spreads into neighbouring ground where colonization from seed does not occur. Similarly, when established in and around heaps of stones, scrap metal or other loose material it survives after their removal. Patches of *U. dioica* in grassland can often be shown to mark the sites of former stacks and piles of hedge clippings. Plants at high altitudes in the Scottish Highlands are said to mark places where a carcass has rotted (N. W. Simmonds). It is a frequent constituent of the sparse ground flora of coniferous plantations.

Occurs occasionally as an epiphyte on willow, ash, hornbeam, oak and poplar (Hegi, *Fl.* 3). Of 3951 records of epiphytes on pollard willows near Cambridge, 306 were of *U. dioica* (Willis & Burkill, 1893).

Occurs on almost all soil types, though absent from waterlogged soils and rare on acid peats. Scott-Elliot (1896) says it is absent from (presumably acid) peat in Dumfriesshire. Its soil requirements have been the subject of some controversy. Olsen (1921) examined a number of habitats in Denmark and showed that all had a soil of high nitrate content. Plants grown in sand culture with varying amounts of nitrate added, up to 50 mg./l. of sand per week (the maximum used), showed increased growth (measured by height and wet and dry weights) with increasing nitrate content. He also showed that nitrogen must be present in the culture solution as nitrate, ammonium being toxic. On the basis of these observations he suggested that the nitrifying power of the soil is a controlling factor in the occurrence of *U. dioica*.

Bates (1933) denied the importance of high nitrifying power, and pointed out that the substratum is often of manifestly low nitrifying power, e.g. sand and gravel heaps. He showed that if young rhizomes are exposed to the light the shoots arising from them are stunted, and the leaves small and yellow, and suggested that protection of the rhizomes from the light until the shoots and leaves have developed is necessary for successful growth. The young rhizomes are incapable of penetrating a compacted substratum, and thus the rhizomes produced by seedlings germinating on a stiff soil remain exposed to the light and fail to develop normal shoots. He suggested, therefore, that the controlling factor is the physical nature of the substratum. He explained the occurrence of *U. dioica*

at the foot of walls of stables, etc., commonly supposed to be due to a high nitrate content derived from urine, by the absence of treading close to the walls.

These two views are not entirely contradictory: Bates considered mainly the establishment of plants, Olsen rather the performance of plants already established or in the artificial conditions of sand culture. Neither author considered the importance of germination conditions in determining distribution. At least under laboratory conditions (see VIII (*d*) below), seed requires thorough soaking and exposure to sunlight or temperature change (not necessarily coincidental with the soaking) before germination occurs. The occurrence of seedlings in the field is associated with sites that have been very wet and exposed to full sunlight, at least in the spring, e.g. on the sites of puddles in woodland clearings. One clear case is of a south-facing, slightly overhanging rock where there was a line of seedlings where water dripped from the rock on to the bare soil beneath (Millers Dale, Derbyshire).

Once established the texture of the soil is probably important in determining vegetative extension, though the inability of the rhizomes to penetrate compacted soils is not as absolute as Bates postulated. Slow spread does occur even in grassland on clay soils. The importance of nitrifying power of the soil requires further investigation. Olsen worked with closed communities where ability to produce luxuriant growth is more important in ensuring survival than in open communities.

Olsen (1921) quotes a case where phosphate content of the soil was possibly limiting. Two sample areas 4 m. apart had soil phosphate contents of 2·6 and 0·4 mg. PO_4/l. respectively. The former bore well-developed *U. dioica*, the latter none. He does not say whether there had been time for vegetative spread from the first area to the second after initial establishment.

Olsen (1921) found a pH range of 3·6–7·3 (electrometric) in the areas he examined in Denmark. A small number of samples examined in Britain have ranged from 6·4 to 7·5 (colorimetric), but there is no reason to suppose that these are the limits.

Olsen (1921) gives limits of light tolerance as: maximum, full daylight; optimum, 10–20% full daylight; minimum, 5–10% full daylight.

III. *Communities.* (i) *Fen carr.* Principal associated herbs:

	(1)	(2)	(3)	(4)
Urtica dioica	l.a.	l.a.	a.	f.
Caltha palustris	a.	—	a.	—
Epilobium hirsutum	l.a.	—	—	—
Iris pseudacorus	l.a.	—	—	a.
Mentha aquatica	l.a.	—	a.	—
Filipendula ulmaria	f.	f.	f.	—
Galium palustre	f.	f.	—	—
Dryopteris dilatata	—	f.-a.	f.	—
Agrostis stolonifera	—	—	f.	l.v.a.
Cirsium palustre	—	—	f.	—
Holcus lanatus	—	—	f.	—
Poa annua	—	—	f.	—
Ranunculus repens	—	—	f.	—
Rubus caesius	—	—	—	v.a.
Thelypteris palustris	—	—	—	v.a.
Calystegia sepium	—	—	—	a.
Lysimachia vulgaris	—	—	—	a.
Symphytum officinale	—	—	—	f.
Hypnum cuspidatum	—	—	—	a.
Mnium affine	—	—	—	f.

(1)–(3) Sweat Mere, Shropshire (Clapham in Tansley, *Br. Isl.* p. 466). (1) Bare mud in Alnetum-glutinosae. (2) On tussocks of *Carex paniculata* in Alnetum-glutinosae. (3) In Betulo-Alnetum.

(4) Developing carr at Wicken Fen, Cambridgeshire. Plants colonizing the bare ground after suppression of *Cladium mariscus* (Tansley, *Br. Isl.* p. 659).

(ii) *Pedunculate oakwood.* Buff Wood, Cambridgeshire. Associated species of the ground flora:

Urtica dioica	a.	Arum maculatum	o.
Mercurialis perennis	d.	Eurhynchium piliferum	
Hedera helix	a.-l.d.	Mnium undulatum	
Galium aparine	a.	Porotrichum alopecurum	
Scilla non-scripta	f.		

(iii) *Ashwood.* Seral ashwood on chalk, Chilterns. Associated species of the ground flora (Watt, 1934):

	Immature consocies	Mature consocies
Urtica dioica	l.d.	o.-l.a.
Fragaria vesca	f.-a.	—
Viola hirta (agg.)	f.	—
V. sylvatica	f.	—
Geum urbanum	o.-f.	o.-f.
Mercurialis perennis	a.-l.d.	d.
Circaea lutetiana	f.	l.a.
Asperula odorata	f.-a.	—

Together with relicts from chalk grassland.

Harley (Tansley, *Br. Isl.* p. 433) found it locally abundant in ashwood with a rich flora in a rocky limestone ravine at Ling Ghyll, Yorkshire. Evans (1945) found it locally abundant on 'soil of medium dampness (pH up to 5·6)' in an upland ashwood on basic igneous rock.

(iv) *Hawthorn scrub.* Ross (Tansley, *Br. Isl.* p. 482) found only five herbaceous species under fully developed hawthorn canopy on abandoned arable land on Chalky Boulder Clay, including *Urtica dioica*, *Galium aparine*, *Mercurialis perennis*, *Primula veris* and *Viola hirta.*

(v) *Larch plantation.* On Lias clay, Newnham, Warwickshire. Principal associated species:

	(1)	(2)		(1)	(2)
Agrostis tenuis	+	–	Myosotis arvensis	+	+
Cerastium vulgatum	–	+	Poa nemoralis	+	–
Cirsium arvense	+	+	P. trivialis	–	+
C. vulgare	–	+	Sonchus oleraceus	–	+
Galium aparine	+	+	Stellaria media	+	–
Holcus mollis	+	+			

(1) Within the plantation.

(2) An adjacent area, originally part of the plantation, which had been felled and bore a rather open vegetation, in which *Urtica dioica* was the most abundant species.

(vi) *Limestone pavement.* Harley (Tansley, *Br. Isl.* p. 433) found it locally dominant in clefts in a mountain limestone pavement near Colt Park, Yorkshire.

(vii) *Upland basic rock.* Evans (1932) found it occasional in a fairly rich flora, including a number of arctic-alpine species, on calciferous pillow lavas at 1500–1700 ft. and 1800–2400 ft. on Cader Idris. The record is interesting, as at such altitudes it is generally closely associated with man and his animals.

(viii) *Boulder beaches.* Near Galway, associated with *Solanum dulcamara, Scrophularia aquatica, Glaucium flavum,* and *Rumex crispus* (*Bot. Irl.* p. 364).

(ix) *River bank.* Newbury, Berkshire, just above water-level. Associated with *Alisma plantago-aquatica, Chrysanthemum parthenium, Lycopus europaeus, Parietaria diffusa* and *Phalaris arundinacea.*

(x) Vevers (1936) records it in several unusual habitats on Ailsa Craig:

	(1)	(2)	(3)		(1)	(2)	(3)
Urtica dioica	o.	f.	v.a.	Carduus crispus	—	—	f.
Melandrium dioicum	d.	o.	a.	Galium saxatile	—	—	f.
Poa annua	f.	—	a.	Senecio jacobaea	—	—	f.
Athyrium filix-foemina	—	f.	—	Umbilicus pendulinus	—	—	f.
Pteridium aquilinum	—	o.	f.	Lycopsis arvensis	—	—	o.
Teucrium scorodonia	—	—	d.	Urtica urens	—	—	o.
Cardamine hirsuta	—	—	v.a.	Erodium cicutarium (agg.)	—	—	r.
Holcus mollis	—	—	a.	Sambucus nigra	—	—	r.

(1) Soil rich in guano at the foot of bird cliffs.
(2) Under boulders on scree slopes.
(3) Foot of cliffs (talus slopes, 30–60°).

IV. *Response to biotic factors.* Will not withstand repeated cutting. Cutting whenever the new shoots reach a height of 6–12 in. is recommended as a means of eradicating it from arable and grassland (Ministry of Agriculture and Fisheries, 1939). According to Asherson & Graebner **4**, it is eaten greedily by many animals, e.g. cattle. This is not true in Britain, where cattle are rarely seen to eat it. It is avoided by rabbits, and may be seen standing up above the closely cropped vegetation in rabbit-infested areas. Bates (1933) states that it may be destroyed by continued trampling by cattle.

V. (*a*) *Gregariousness.* Frequently in large patches, forming under favourable conditions an almost pure stand.

(*b*) *Performance in various habitats.* In full daylight or very dry conditions growth is rather stunted, the shoots averaging 1–2 ft. (3–6 dm.) in height, and the leaves are often small, but flowers are generally produced freely. In moderate shade the shoots average 2–4 ft. (6–12 dm.), with numerous flowers. Under the most favourable conditions of light and soil shoots may reach 6 ft. (1·8 m.). In deep shade there is often abundant vegetative growth but few flowers.

(*c*) *Effect of frost, drought, etc.* The shoot tips may die back after early frosts in the autumn, and such frosted shoots may produce lateral branches before their death later in the autumn.

VI. (*a*) *Morphology.* New rhizomes are produced in late summer or autumn either from older rhizomes or from the base of aerial shoots. They continue to grow at or just beneath the soil surface until the death of the aerial shoots, when they turn up to form new shoots (Fig. 2). (In very loose soils rhizomes may be found at greater depths, up to 1 ft. (3 dm.) or more.) Young rhizomes are reddish in colour and bear stinging hairs and scale leaves with a small rudimentary lamina and large stipules, broader than those of the aerial leaves. The stipules survive after the death of the lamina. Roots arise immediately above the stipules (four per node), frequently immediately below some or all of the stipules and occasionally between the nodes. The roots branch profusely and form numerous fine laterals. Older rhizomes and roots have a yellow cork layer.

(*b*) *Mycorrhiza.* No information.

(*c*) *Perennation; reproduction.* The new shoots produced in the autumn (see (*a*) above) continue growth until about 6 in. high. In most habitats in England, in most years at least, these shoots survive the winter and resume growth the following spring. Thus, although generally described as hemicryptophyte, in England it is more usually chamaephyte. In more northern parts of its range it may be regularly hemicryptophyte.

Vegetative spread is by means of the rhizomes; Kerner (1895, p. 797) estimated the annual increment at 35–45 cm. (approx. 14–18 in.).

The age of the plant at first flowering is not known, but it does not flower in the first year. Abundant seed is produced every year, but the number of seedlings varies greatly from year to year. Alternating periods of rain and sunny weather in the spring appear to favour their development.

(d) *Chromosome number and sex mechanism.* $2n = 48$ (Heitz, 1926), $2n = 52$ (Fothergill, 1936). Dr K. Mather says (*in litt.*): 'The chromosome numbers of the genus seem to show two series based on $x = 12$ and $x = 13$ respectively. In this case it would not be surprising if there were two tetraploid forms sufficiently similar to be confused when only morphological characters are used in diagnosis.' Meurman (1925 *a, b*) suggests the probable existence of a pair of unequal sex chromosomes in the male plant. Strasburger (1910) selfed female plants bearing occasional male or hermaphrodite flowers and obtained an exclusively female progeny.

(e) *Physiological data.* No information.

Fig. 2. *Urtica dioica* L. Portion of plant collected in November 1947. *A*, remains of 1947 shoot. *B*, rhizomes produced in the autumn of 1947, turning up to form 1948 shoots.

VII. *Phenology.* Times of appearance of new rhizomes and shoots, see VI (*a*) and (*c*) above. Darwin (1919, 1921) gives dates of flowering for four consecutive years in Gloucestershire:

Male first flowering	June 5	May 25	June 2	May 29 ('average')
Female first flowering	June	May	June 30	—

Blomefield (1903) gives earliest, latest and average dates of flowering in Cambridgeshire for six years between 1820 and 1849 (years of observation and sex of flowers are not stated): earliest date, 28 May; latest date, 16 June; average date, 6 June. Hegi (*Fl.* **3**) says male plants flower rather later than female. In 1943 seed was being shed in Warwickshire by 20 June. Viable seeds may remain on dead shoots up to December or January. Occasional seedlings may be found in the autumn (it is not known whether such seedlings survive the winter), but the main production of seedlings occurs in the spring.

VIII. (*a*) *Floral biology.* Normally wind-pollinated. The immature stamens are bent towards the centre of the flower. When the anthers are mature the stamens straighten

explosively, scattering the pollen. Strasburger (1910) made counts of pollen and flowers on a shoot bearing four inflorescences at each of six nodes and gives the following average figures:

Pollen grains per anther	1,500
Pollen grains per flower	6,000
Flowers per node	1,274
Total no. of pollen grains produced by shoot	44,892,000

Occasional pollination by insects may occur. Knuth (*Poll.* 3) gives *Brachypterus urticae* (Fab.) and *Syrphus arcuatus* Fall. as insect visitors. A. E. Wade (*in litt.*) records finding *Brachypterus glaber* (Steph.) apparently pollinating.

Reproduction amphimictic; it was shown by Modilewsky (1908) and confirmed by Strasburger (1910) that female plants bearing no male or hermaphrodite flowers would not set seed when protected from pollination.

(*b*) *Hybrids.* Asherson & Graebner (**4**) consider *Urtica oblongata* Koch to be a hybrid with *U. urens* (presumably on morphological grounds only).

(*c*) *Seed production and dispersal.* Fruits are single-seeded. No information on number of fruits per plant. The hispid perianth segments are persistent, causing the fruits to adhere to 'fur, feathers and cloth' (Ridley, *Disp. plts.*) and probably also assisting in wind dispersal. Both individual fruits and parts of inflorescences may adhere to clothes, etc., dropping off as they become dried. Heinitz (quoted in Ridley, *Disp. plts.*) describes dispersal in the excrement of cattle, fallow deer and magpie in Sweden. Ridley (*Disp. plts.*) notes a plant 8 ft. up a wall, almost certainly derived from a fruit carried by wind. Fruits in water sink in less than a week (Guppy, 1906).

(*d*) *Viability of seeds; germination.* Under laboratory conditions (on moist filter-paper in Petri dishes) germination is greatest when exposed to direct sunlight. Under uniform low light and constant temperature little germination occurs, but further germination follows exposure to either higher or lower temperature; final germination is not, however, as great as when exposed to sunlight. There is slight evidence that under low light and constant temperature the presence of nitrate may also increase germination slightly. In the dark no temperature treatment has been successful in producing germination. There is some evidence that the longer the period of soaking before exposure to sunlight the greater is the period of exposure needed to produce an equivalent percentage germination. With exposure to sunlight different batches of fruits (both from different localities in the same year and the same locality in different years) have varied rather widely in final germination, from 26 to 94 % for trials in the same year as fruits were collected. Stored dry viability of fruits does not decrease with age for the first two years at least; one batch of fruit collected in 1945 (not tested in 1945) gave up to 98 % germination in June 1947.

For germination under natural conditions, see II above.

(*e*) *Seedling morphology.* Achene splits at the apex and radicle appears. Hypocotyl elongates and straightens, sometimes withdrawing the cotyledons from the remains of the achene, sometimes carrying the latter up with them. Cotyledons oblong, emarginate, rather succulent (Fig. 3).

(*f*) *Effective reproduction.* Increase in area of patches once established from seed is in most habitats entirely vegetative.

IX. (*a*) *Animal feeders or parasites.* See *Urtica* L.

(*b*) *Plant parasites.* Attacked by *Cuscuta europaea* L. For fungi, see *Urtica* L.

(c) *Diseases*. Patches are often found in which all the shoots show chlorosis of the leaves. The cause is not clear, but it is possibly due to exposure of the rhizomes (cf. II above). See also section on fungi in *Urtica* L.

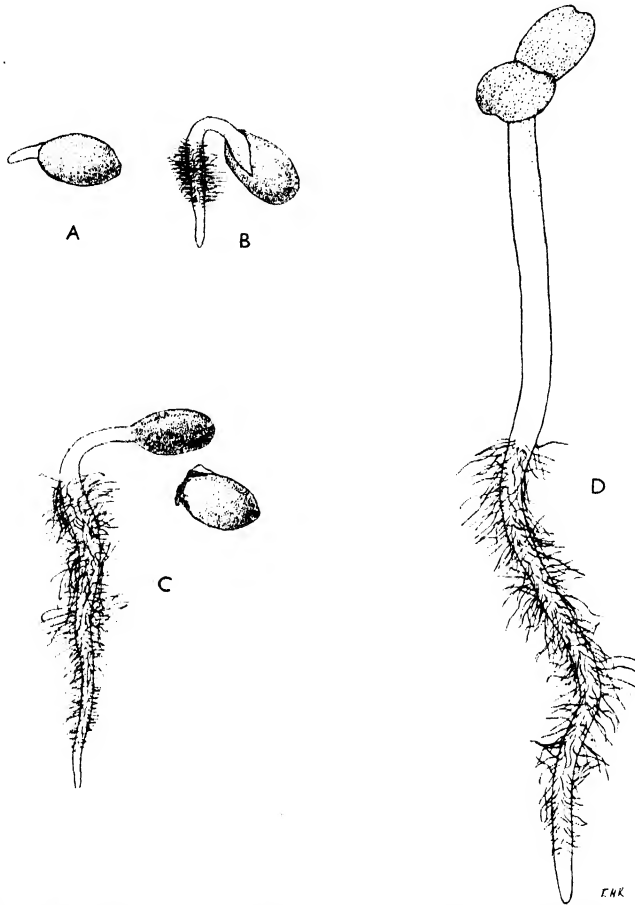X. *History*. See section on fossil records in *Urtica* L.

Fig. 3. Seedlings of *Urtica dioica* L. × 8. A–D. Stages in germination.

Lond. Cat. (Ed. 11) No. **1732**

Urtica urens L.

P. GREIG-SMITH

An annual herb, almost glabrous except for stinging hairs. Stem erect, simple or more generally much branched. Leaves opposite, petiolate, elliptic, occasionally orbicular, deeply inciso-serrate. Stipules small (c. 1 mm.) ovate-lanceolate, acute. Inflorescences (four per node) spikes of mixed glomerules, arising in pairs from the leaf axils (often in addition to a branch). Achenes larger than in *U. dioica* (c. 1·5 × 1 mm.). Stem, leaves and inflorescences bearing stinging hairs.

Shows little variation. Druce (1928) records a variety *parvifolia* Dr.

A common species of cultivated ground and disturbed habitats, especially on light soils.

I. *Geographical and altitudinal distribution.* Recorded from all British and Irish vice-counties. Frequent in suitable habitats. There is a specimen from Radnorshire (v.c. 43), the only vice-county for which a published record is lacking, in Herb. Nat. Mus. Wales (A. E. Wade).

Occurs throughout Europe, except Spitsbergen, Jan Mayen, Novaya Zemlya and Arctic Russia, reaching 71° N. in Scandinavia (Hermann, 1912), over almost the whole of Asia,

Fig. 4. *Urtica urens* L. Vice-comital distribution in the British Isles and (inset) distribution in Europe.

and in Arabia, North Africa, Abyssinia, South Africa, Canary Isles, Madeira, Australia, New Zealand and North and South America. Probably adventive outside Europe and temperate Asia.

A more markedly lowland species than *U. dioica* and like that is always associated with man or his animals at higher altitudes. Ascends to 1650 ft. (503 m.) in East Allendale (Baker & Tait, 1868), 1525 ft. (465 m.) in Teesdale (Wilson, 1938), 1050 ft. (320 m.) in north Yorkshire (Baker, 1906), 1170 ft. (357 m.) at Hen Hafod, Cardiganshire (Burkill & Willis, 1894), 1500 ft. (457 m.) in Atholl (White, 1898) and 1200 ft. (366 m.) in Aberdeenshire (Dickie, 1860). In Europe ascends to 7612 ft. (2320 m.) in Munstertal, Graubünden

(Braun-Blanquet & Rübel, 1933), 7000 ft. (2134 m.) in Valais (D'Angreville, 1862) and over 6562 ft. (2000 m.) in Tirol (summit nominally 2215 m. (7268 ft.), Hegi, *Fl.* 3) and Caucasus (Aschers. & Graebn. 4).

II. *Habitat.* More restricted than *U. dioica.* In Britain the only natural habitat appears to be on sand near the coast. In coastal counties it is less common in all habitats inland than near the coast, e.g. Devon (Martin & Fraser, 1939), Kent (Hanbury & Marshall, 1899) and Sussex (Wolley-Dod, 1937). Martin & Fraser comment '...grows luxuriantly on coastal headlands, as at Berry Head', but do not state whether in natural or disturbed habitats. Elsewhere it is, like *U. dioica,* a follower of man, occurring round farm buildings, on waste ground, sand heaps, etc., and as an abundant weed of arable land. As an arable weed it frequently forms a dense pure stand, particularly among crops which receive several cultivations, e.g. potatoes. It is much less common on heavy than on light soils. It is said to be nitrophilous (Braun-Blanquet & Rübel, 1933), and, by agriculturalists, an indicator of lime deficiency (Ministry of Agriculture & Fisheries, 1939). It is intolerant of heavy shading.

III. *Communities.* The following lists are typical of the associated species on cultivated ground:

	(1)	(2)	(3)		(1)	(2)	(3)
Capsella bursa-pastoris	+	+	−	Polygonum convolvulus	+	−	−
Chenopodium album	+	−	−	P. persicaria	+	−	−
C. bonus-henricus	+	−	−	Potentilla anserina	+	−	−
Convolvulus arvensis	−	−	+	Senecio vulgaris	+	−	+
Erysimum cheiranthoides	+	−	−	Sinapis arvensis	+	−	−
Fumaria officinalis (s.l.)	+	−	−	Solanum nigrum	+	−	−
Holcus mollis	−	−	+	Sonchus asper	+	−	−
Poa annua	−	−	+	Stellaria media	+	−	+
Polygonum aviculare (agg.)	+	−	+	Veronica persica	−	−	+

(1) South-east Fens (composite list).   (2), (3) Iver, Bucks., on light soil.

Vevers (1936) records it as occasional at the foot of cliffs on Ailsa Craig (see *U. dioica,* III (x), for list).

IV. *Response to biotic factors.* Like *U. dioica* it is avoided by rabbits.

V. (a) *Gregariousness.* Where competition is slight, as in well-cultivated fields of crops such as onions which cast little shade, the ground between the crop plants may be covered by an almost pure stand of *U. urens.* Elsewhere it generally occurs as isolated plants or small patches.

(b) *Performance in various habitats.* Under favourable conditions of slight competition and light soil, plants that germinated early in the year may reach a height of 30 in. (76 cm.) and diameter of 10–12 in. (25–30 cm.).

(c) *Effect of frost, drought, etc.* No information.

VI. (a) *Morphology.* A vertical tap root, occasionally forked, bears numerous branching, descending laterals, some of which develop much more strongly than others.

(b) *Mycorrhiza.* No information.

(c) *Perennation; reproduction.* Therophyte. Plants may flower and set seed before the cotyledons have withered, when only 3–4 in. (8–10 cm.) high. Vegetative growth does not cease at flowering, however, and further inflorescences are produced; flowering continues until the plants are killed by autumn frosts. Young plants found late in the year are probably derived from seed produced earlier in the same year.

(d) *Chromosome number.* $2n = 24$ (Fothergill, 1936).

(e) *Physiological data.* No information.

VII. *Phenology.* Blomefield (1903) gives earliest, latest and average dates of first flowering in Cambridgeshire for five years between 1820 and 1849 (years of observation not stated): earliest date, 9 April; latest date, 19 July; average date, 31 May. In 1944 pollen was still being released on 10 October. In 1943 small plants near Cambridge bore well-developed fruits on 2 May. Fruits shed early in the year probably germinate at once; those shed later germinate in the following spring.

VIII. (*a*) *Floral biology.* Wind-pollinated, the pollen being scattered by an explosive mechanism like that of *U. dioica.* Protogynous.
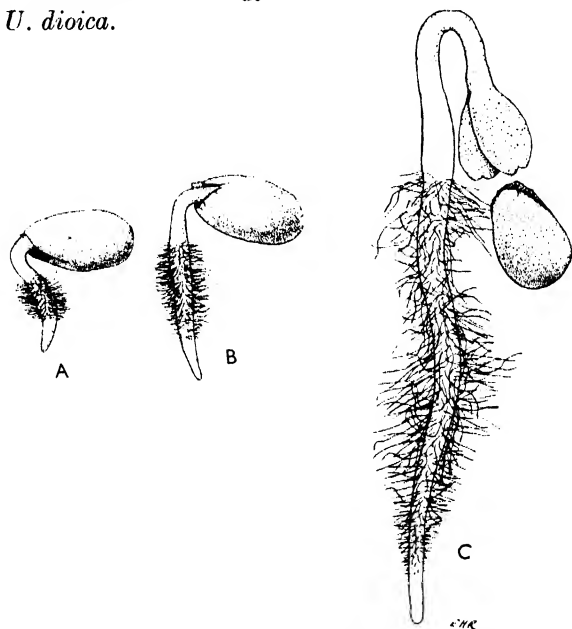
(*b*) *Hybrids.* See *U. dioica.*

Fig. 5. Seedlings of *Urtica urens* L. ×8. A–C. Stages in germination.

(*c*) *Seed production and dispersal.* Fruits are single-seeded with persistent perianth segments, similar to those of *U. dioica.* No information on number of fruits per plant. Dispersal is similar to that of *U. dioica.* Heinitz (quoted in Ridley, *Disp. plts.*) describes dispersal in dung of cattle in Sweden. The fruits do not float (Praeger, 1913).

(*d*) *Viability of seeds; germination.* Fruits collected in 1944 and sown on moist filter-paper in Petri dishes gave 15 % germination in an incubator at 26° C. in December 1944, 46 % in incubator at 27° C. and 5 % at room temperature in February 1945, and 11 % at room temperature in January 1946. Germination started in about 4 days and continued for from 8 to 23 days, except in the last experiment where germination started after 14 days and continued for 2 months.

(*e*) *Seedling morphology.* Similar to *U. dioica,* but cotyledons ovate rather than oblong (Fig. 5).

(*f*) *Effective reproduction.* Entirely by seed.

IX. (*a*) *Animal feeders or parasites.* See *Urtica* L.

(*b*) *Plant parasites.* Attacked by *Cuscuta europaea.* For fungi, see *Urtica* L.

(*c*) *Diseases.* None recorded.

X. *History.* See section on fossil records in *Urtica* L.

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CUSCUTA L.

BERNARD VERDCOURT

There are two native British species of the genus, both belonging to the section *Eucuscuta* Engelm. of the subgenus *Cuscuta* s.s., namely, *C. europaea* L. and *C. epithymum* (L.) Murr. The subgenus *Cuscuta* is distinguished from all the other subgenera of *Cuscuta* by the distinctly linear styles and linear stigmas. The section *Eucuscuta* is distinguished from the other sections of the subgenus by its regularly circumscissile capsule.

The number of aliens which have occurred in Britain is uncertain since in the past species of this genus have been named by what is little more than guesswork. The following have been definitely recorded.

Subgenus *Cuscuta* s.s. section *Eucuscuta*:

C. epilinum Weihe. Europe.

C. planiflora Ten. Mediterranean.

C. approximata Bab. Southern Asia. The type of this species was raised in Britain from seeds imported from Afghanistan.

Subgenus *Grammica* Engelm. section *Cleistogrammica* Engelm.

C. suaveolens Seringe. Native to southern South America, but now cosmopolitan or nearly so.

C. australis subspecies *tinei* (Insenga) Yunck. Europe and India.

C. campestris Yunck. Western U.S.A., becoming cosmopolitan.

The position of the form known as *C. trifolii* Bab. will be discussed under *C. epithymum*. There can be no doubt that many of the specimens referred to this form in the past have been aliens.

Cytology. The basic chromosome number is 7 (cytological information taken from Finn, 1937).

Habit and life-form. All the species of *Cuscuta* are, except for a brief period after germination, total parasites. The young seedling possesses a small well-defined root but bears no cotyledons. The growing point circumnutates until a suitable host is found for attachment, and once the latter is successfully accomplished the lower part of the seedling perishes. The maximum length of life of the seedling without a host varies with the size of the species, but it may be as long as seven weeks. The adult plant is a vigorous twiner. It is a morphologically and anatomically specialized parasite, leaves being minute or absent. The stem, however, is well developed compared with other parasites. This is related to the mode of attachment to the host and allows rapid spreading. A certain amount of chlorophyll is present in a few species and these are partially autotrophic, though the amount of assimilation is totally inadequate for the plant's requirements.

Duration. All temperate species are annuals, but some tropical ones are perennials.

Flowers. Small, sub-sessile in globular clusters, or stalked in lateral cymes. Mirande (1901) discusses the inflorescence in the group and concludes that the fundamental type occurring is the uniparous scorpioid cyme, and that other types have been produced by the contraction of the internodes. Flowers usually yellowish with a pink tinge. Alternating

with the lobes of the corolla are the epistamineal scales, which are of great taxonomic value. The function and even the origin of these scales are doubtful. They appear to be outgrowths of the filaments, but Cunningham (1898) considers that they are derived from the corolla itself.

Self-pollination appears to be the rule. Both Yuncker (1921) and the writer have failed to observe any insect visitors. W. D. Pierce (1939) records a number of insects from the flowers of various Californian dodders. Most of these have proved to be pollen or seed feeders and are therefore destructive. Several, however, including *Bruchus* sp., *Melano-phthalmus* sp., and *Scymnus* sp., probably do act as pollinators. Further observations on British material are very necessary. Müller (1883) states that the flowers are visited by *Sphegidae* and in the absence of insects are self-pollinated. Knuth (Poll. **3**) states that the flowers are usually homogamous, and that cleistogamy is frequent. Autogamy is brought about by the convergence of the filaments on to the stigmas and frequently takes place pseudocleistogamously when the flowers are closed during rainy weather (Kerner, 1894). Adaptations for entomophily are rarely present, but three or four tropical species are fragrant and Müller (1883) states that in *C. epithymum* 'honey is secreted by the lower part of the ovary and is sheltered by the scale-like appendages of the corolla'.

Ecology. Various. Many of the species show a specific preference for certain host plants, which range from small herbs to trees. Certain ecological factors independent of those which affect the host are sometimes important, probably in connection with the brief free-living period in the parasite's life history. Geographical distribution is in general world-wide, but the genus appears to be absent from the Philippine Islands. A small group of species have become pests of arable crops and have been distributed throughout the world mixed with seed. For instance 2% of tested English clover seed samples have been found to contain dodder seeds and in the case of foreign seed a percentage as high as 85 has been recorded (Min. of Agric. Ad. Leaflet No. 59, 1931).

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INSECTS AND FUNGI ASSOCIATED WITH *CUSCUTA*. INSECTS (B. Verdcourt)

COLEOPTERA

CURCULIONIDAE: Weevils of the tribe *Smicronychini* are hyperparasites of species of *Cuscuta* throughout the world. The larvae form galls in the stems (more rarely in the flowers) and either pupate in these or in the ground. Four species of *Smicronyx*, all of which are very rare or rare, are found in the south of England, namely *S. coecus* Reich., *S. jungermanniae* Reich., *S. seriepilosus* Tourn., and *S. reichii* Gyll. *S. jungermanniae*

forms ellipsoidal galls in the stems of *C. europaea*, and the larvae pupate in the ground. The other three species are apparently found on all British dodders, but published records of these beetles usually omit the precise identification of the host. *S. coecus* is recorded on *C. europaea*, *S. reichii* on *C. europaea* and *C. epilinum*, and *S. jungermanniae* on *C. epithymum* by Fowler (*Coleopt.* **5**, 281).

FUNGI (B. VERDCOURT)

No records of parasites of the British species could be found. The writer has found *Botrytis cinerea* Pers. ex. Fr. on *C. europaea*. The only two fungal parasites of *Cuscuta* which have been recorded are *Dendryphium mac-owanianum* Thüm, recorded as a parasite of the S. African species *C. cassytoides* Nees. (*Sacc. Syl.* **4**, 490), and a species of *Protomyces* recorded from the American *C. gronovii* Willd. (Peck, 1874).

VIRUS DISEASES

Two papers have recently been published concerning the transmission of virus by dodder (Johnson, F., 1941; Bennett, 1944).

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L.C. (Ed. 11) No. **1420**

Cuscuta europaea L.

BERNARD VERDCOURT

Subgenus *Cuscuta* s.s., section *Eucuscuta* Engel. Plant perfectly glabrous, much branched. Stems 0·5–0·9 (−1·0) mm. in diameter. Older parts brownish crimson, younger parts pale whitish yellow. The stem is quite elastic and capable of stretching about 10% of its length. The leaves are reduced to very small scales, bearing stomata. Flowers sub-sessile, in globular clusters which average 1 cm. in diameter, expanding to 1·2 to 1·5 cm. after fertilization. Flowers 2–3 mm. long, mostly 4–5 partite; pedicels short and thick. Calyx and calyx-tube fleshy, their epidermal cells being large and rectangular; calyx lobes obtuse, ovate, shorter than the corolla-tube, mostly yellow-green with a crimson tinge at the apex. Corolla campanulate, lobes mostly triangular, obtuse and spreading, whitish, tinged with very pale pink. Epistamineal scales thin, variable in shape, and becoming split at the base as the capsule develops. They are adpressed to the corolla and scarcely reach the base of the stamens (Fig. 1). Stamens shorter than the corolla, inserted. Stigmas usually crimson, equalling styles, together shorter than the globular ovary. Capsule globose, slightly conical, circumscissile. Corolla persistent. Seeds yellow-brown, turning blackish, surface granular, ellipsoidal but variable, attaining 1·25 by 1·1 mm.

The species is characterized and readily separated from the other British species by the thick stem, small adpressed scales, inserted stamens, and fleshy calyx. As Yuncker (1932) points out, it is difficult to accept varieties based on scale characteristics since the

normal variation of these extends over a considerable range, and extremes may be found in one inflorescence. Var. *nefrens* Fr., stated to bear no scales, is recorded from Britain (Syme, 1866), but is imaginary (Verdcourt, 1947); var. *viciae* Koch has the scales more cut than usual, but is a doubtful variety. Certainly British specimens answering to this description have occurred—mostly in untypical habitats and having every appearance of being introductions (Verdcourt, 1948). The typical form is distinguished as var. *genuina* Beyer forma *typica* Rouy, and there is a var. *conocarpa* Engel. possessing a more markedly conic capsule than the typical form and having the same distribution. In the writer's opinion none of these names is justified and they are better dropped. Flowers with an abnormal number of styles are not uncommon. Three styles are frequently present and one flower was examined which contained five, three being basal branches of the other two.

I. *Geographical and altitudinal distribution.* Essentially a southern species in Great Britain, it is recorded from thirty-nine vice-counties in England and one in Wales. Some of these records, though accepted by Druce (*Comit. Fl.*), are doubtful according to botanists
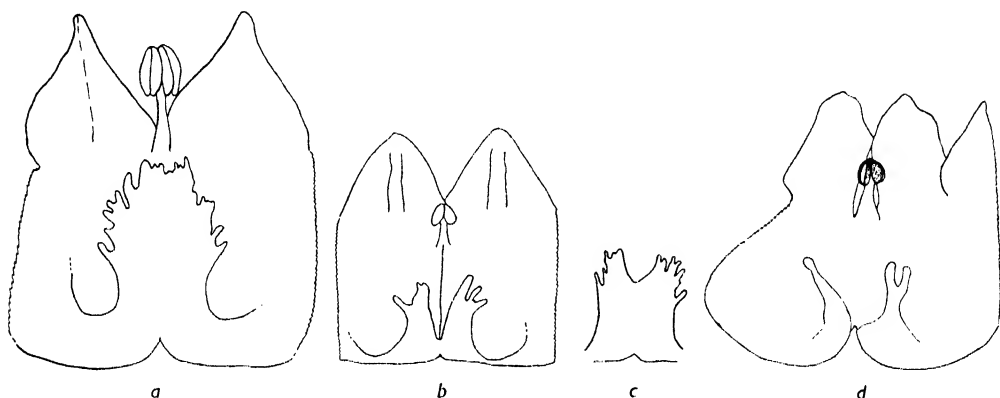

Fig. 1. Epistamineal scales of (a) *Cuscuta epithymum*, (b) *C. europaea* (from an unfertilized flower), (c) ditto to show variation, and (d) *C. europaea* (from corolla of flower after fruit has matured).

living in the areas concerned. It is doubtfully recorded from three other northern counties, but has occurred in Scotland as an introduction or casual on several occasions (Verdcourt, 1948). Its distribution in England follows the main rivers. Apparently absent from Cornwall and very rare in Devon and Dorset. The Bristol Avon valley is its main centre in the west. The plant is particularly frequent in the Thames valley and has occurred by the river in every county through which the Thames flows. It is also frequent in the Mole valley in Surrey, and the latter county is probably the one in which it is commonest. In the other southern counties up to the Wash it occurs sparingly by rivers and by streams. North of the Wash it is recorded mainly as an introduced species though it has occurred in typical habitats in Leicestershire.

Throughout Europe to 63° 20′ N. in Norway (Lid, 1944), to 63° in Finland, (Kew Herb.) and 64° N. (Västerbottan) in Sweden (Lindmann, 1918). Siberia, Northern Africa, and temperate Himalaya (Collet, 1902). Casual in N. America (Yuncker, 1921).

A survey of over 100 authentic records shows that in Britain the plant grows at altitudes ranging from 0–150 ft. (0–46 m.) (95%), with a few at 150–400 ft. (46–122 m.) (5%). Wilson (*Alt. Range Br. Pl.* p. 59) gives 'lowland in England', i.e. 0–1000 ft. (0–305 m.).

In Europe it occurs at 3200 ft. (975 m.) in Albania, 3760 ft. (1150 m.) in the Tirol, 1650 m. in Graubünden (Switzerland) (Braun-Blanquet & Rübel, 1934), and 5500 ft. (1680 m.) in Epirus (Kew Herb.). West of Yatung in Tibet it was found at 10,000 ft. (3048 m.) by F. S. Chapman. Collet (1902) and Hooker (1890) record it as ranging from 5000 to 10,000 ft. (3048 m.), in the Himalaya.

II. *Habitat. C. europaea* shows a strong preference for the vicinity of running water and generally occurs in hedges and the luxuriant herbage or scrub on alluvial soils by rivers and streams, mostly in shady places.
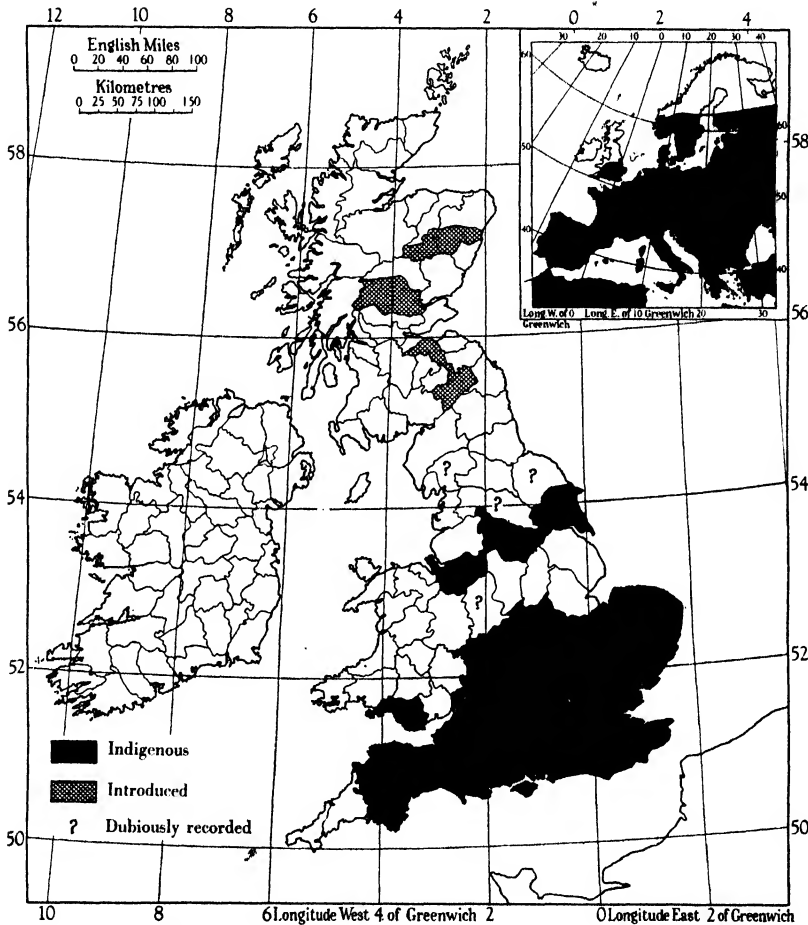

Fig. 2. *Cuscuta europaea* L. Vice-comital distribution in the British Isles and (inset) distribution in Europe.

III. *Communities and host plants.* Chiefly in nitratophilous riparian communities characterized by *Urtica dioica, Epilobium hirsutum, Galium aparine, Humulus lupulus, Conium maculatum, Solanum dulcamara, Cirsium arvense, Carduus crispus,* etc., and commonly in shade from overhanging trees or bridges. Many works state that any plant is a suitable host, e.g. Bentham, 1878: Yuncker, 1921 and 1932, but in this country, at the limit of its natural range, *C. europaea* undoubtedly favours the common nettle, *Urtica dioica.* The type specimen in the Linnean Herbarium is on nettle, and Gerard (1597), who

first noted the plant as British, gave its host as nettles; while J. E. Lousley and the author find that nettles have clearly been the primary host in all the localities they have studied at first hand. The hop, *Humulus lupulus*, appears however to be a frequent host. The accompanying table shows the results of an investigation of 102 herbarium specimens confirmed as being *C. europaea*.

Host of C. europaea (*from herbarium specimens*)

	Urtica dioica	Humulus lupulus	Other hosts	None	Total
No. of specimens	62	23*	17†	6	102

* In six cases *Urtica* and *Humulus* preserved together as hosts.

† In only two cases was *Urtica* definitely known to be absent from locus, and in these *Humulus* was present.

Important hosts beside nettle and hop are the species listed in the first paragraph of this section, and to them may be added *Brassica nigra, Angelica sylvestris, Heracleum sphondylium, Convolvulus arvensis, Calystegia sepium, Sparganium ramosum, Glyceria maxima, Atriplex* sp., *Cirsium vulgare, Achillea ptarmica*, and *Equisetum arvense*; and amongst the woody plants, *Prunus spinosa, Rubus* spp., *Crataegus monogyna, Acer campestre, Cornus sanguinea*, and *Salix* spp. The parasite was observed twining on *Hedera helix*, but without penetration by the haustoria.

In pot experiments seedlings were found to establish equally well on a wide range of plants, but it has invariably been observed in the field by the writer that nettle and hop are first attacked and that the parasite spreads from them to other species. Since nettle and hop are related taxonomically there is presumably some biochemical basis for the observed preference.

There is little doubt that some records of hosts such as bracken have arisen from a faulty identification of the parasite, another dodder having been misnamed *C. europaea*.

IV. *Response to biotic factors.* There are no recorded instances of the plant having been grazed by stock and its usual hosts are distasteful to animals. Any factors which influence the host, indirectly affect the parasite and may lead to its disappearance. J. W. Haines gives some interesting information concerning the plant growing in a hedge at Hucclecote, near Gloucester. It was first observed there in 1915 and was noted each year up to 1919, on *Humulus*. In 1920 the hedge was severely cut and the *Humulus* disappeared. The dodder made no appearance that year, but reappeared in 1923 preceded by the hops. This happened again in 1933 and 1943, the disappearance in each case being preceded by hedging and the eradication of the host *Humulus*. Since viable seeds of the dodder must have been constantly in the ground this tends to confirm the view that hops or nettles are essential for the preliminary starting stage.

C. europaea usually restricts itself to large and healthy plants and does not cause their death. Small weak hosts such as grass seedlings die or become very chlorotic.

The writer has never seen the plant as a pest of agricultural crops, but references to it on *Vicia* sp. are frequent. In the case of it proving a weed the methods of control noted in the account on *C. epithymum* would be suitable. The Dodder Committee of the International Seed Testing Congress (Degen, 1924) does not mention the species as a pest, but Kerner & Oliver (1894) state that it sometimes ravages hop plantations in Europe.

V. (*a*) *Gregariousness.* Usually in patches extending over about 2–5 sq.yd. of host plants. Such patches may result from a single seedling, but more usually from several. Occasionally on river banks where there are extensive areas of nettle beds it may extend

continuously for distances of up to half a mile, e.g. at Staverton in Wiltshire, by the R. Avon (J. D. Grose).

(*b*) *Performance in various habitats.* Since the habitats are uniform there is little variation in different loci save in the size of the patch. Unless another parasite species is also present there is no factor of competition.

(*c*) *Effect of frost, etc.* The late germination of the seeds safeguards the plant from the majority of frosts. Very early seedlings do not appear to suffer from frost during pot tests out of doors. Drought frequently results in the disappearance of the plant. It made no appearance at Sonning, Berks. in 1945 when a small streamlet dried up near the habitat in which it was abundant in 1944. It must be mentioned, however, that the species often disappears for no apparent reason from a habitat where it was abundant the previous year. The plant is scarcer during years with dry summers, since establishment can only take place under humid conditions.

VI. (*a*) *Morphology.* Roots are only present in the seedling.

(*b*) *Perennation*; reproduction annual (parasite). Once a shoot has become thoroughly attached to the host, it will, even though quite small, continue to grow after severance from the main patch. Longevity about five months. Usually well in flower by the middle of July, i.e. at about 6 weeks old. At Leighton Buzzard, Beds., $5\frac{1}{2}$ weeks (1947). Seeds are produced every year, though, as has been noted, it is often absent for a year or so if conditions are unfavourable.

(*c*) *Chromosome number.* A diploid with somatic number $2N = 14$ (Finn, 1937). Warnstoff gives pollen grain size as $35 \times 22\,\mu$ (Knuth, *Poll.* **3**, 150). 21.7 to 23.3×23.3 to $24.8\,\mu$ (Beds. material). Another lot of Beds. material gave 18 to 21×21 to $22.5\,\mu$.

VII. *Phenology.* For radicle of seedling see VIII (*d*).

The first buds appear at the beginning, and the first flower opens about the middle, of July. Flowering continues to the first week in October, but is often over by the end of September. Fruits are first formed and corollas wither at the end of July; maturation occurs during August and September. Fruit formation continues until October and the plant is usually dead by the end of October.

Non-flowering shoots have not been seen. If, when a new shoot has fixed itself to a host, connection with the main part of the parasite is broken, the flowering of the small shoot is often delayed for several weeks.

Germination in the field is late, occurring about the 1st of June, and the parasite is well attached by the third week in June if a host is found. Late germination is essential to ensure that the host plants are well advanced. Seedlings of the dodder which have become attached to small grass seedlings during pot tests, have caused the death of these seedlings and eventually of themselves. In pot tests carried out at external atmospheric temperatures, a small percentage of seeds (1–3 %) often germinate early. In 1947 3 % germination was obtained at the beginning of April. In 1946 1 % was obtained by the 11th of February. This early germination has not been noted in natural habitats.

VIII. (*a*) *Floral biology.* See *Cuscuta* L. Cleistogamy is frequent. Apomixis is not recorded. Vivipary is not recorded.

(*b*) *Hybrids.* None are known. *C. trifolii* Bab. was claimed by Simkovics (1878) to be a hybrid between *C. europaea* L. and *C. epithymum* (L.) Murr., but this is not tenable on taxonomic grounds.

(*c*) *Seed production and dispersal.* Up to four seeds per fruit. On the average (Beds.

material) three out of four ovules had developed in 41·7%, two out of four in 33·3% and all in 25% of the ovaries examined. Inflorescences contain on the average 26 flowers and thus give rise to 76 seeds. There are usually about 20 inflorescences per metre of stem and thus seed production is about 1520 seeds per metre. A sample of 91 seeds weighed 33·2 mg. giving 0·365 mg. per seed as the mean.

Little conclusive evidence about dispersal is available. Over short distances dispersal is effected by the ramifications of the parent plant. The preference for the banks of running water suggests that water dispersal may be important. Fruiting inflorescences have been observed hanging in the water. The seeds sink in water, but the capsules containing the seeds will float for two days.
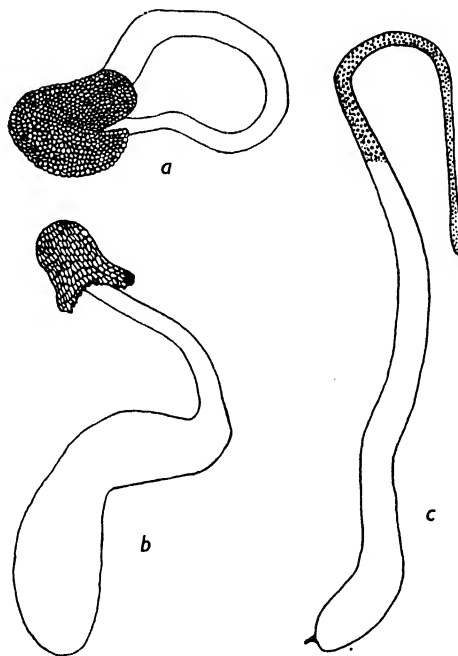

Fig. 3. *Cuscuta europaea* L. *a–c*, stages in germination. × 10.

(*d*), (*e*) *Viability of seeds; germination, etc.* Little information is available. Mirande (1901) gives the figure as about six years. Long (1910) states that the dodder seeds may lie dormant in the soil for 5–6 years. The writer has obtained 30–50% germination with year-old seeds in pot tests. Seeds after seven years' dry storage (from herbarium specimens) gave 3% early germination and 0% in June. Germination was seldom obtained where seeds were buried over half an inch (1·3 cm.) below the surface.

At 12° C. and under favourable conditions of humidity the seeds of *C. europaea* germinate in about eight days (Fig. 3). The radicle, which shows weak positive geotropism, emerges as a small rounded body terminating in a point. It elongates rapidly, as does the 'hypocotyl', which shows strong negative geotropism and is at first hooked distally, but gradually straightens and becomes erect. Its elongation is retarded by light. The hypocotyl extends into the earth at its base for little more than 2 mm. Its elongation reaches a maximum in the first quarter and is small at the summit and in the basal half. The upper part is pale greenish yellow owing to the presence of small amounts of chlorophyll.

Diffuse light and a humid atmosphere are essential for normal development, and the seedling is very sensitive to drought. Even before the remains of the seed fall the tip of the hypocotyl begins extensive but irregular nutating movements, rarely making a complete circle. Mirande (1901), who summarizes previous investigations, states that the young seedlings will twine round dead objects provided the atmosphere is humid, but will not twine round dry material. Pierce (1894) was unable to confirm this and the writer has obtained only slight twining round wet dead objects. Even when a host is available the seedling may not attach itself and indeed may twine round it for a half-circle and later untwine and continue nutating movements. It appears that before attachment can take place a definite stage of irritability and growth must be attained. In pot experiments the hypocotyl was observed to twine once or twice round a young grass seedling about 1 mm. in diameter, but attachment took place only after five to ten days had elapsed. Under natural conditions attachment usually occurs at about 6 in. (15 cm.) above ground level, and on as large a host as a stem of *Urtica dioica* no twining occurs, the tip alone becoming attached, often by only one haustorium. The primary haustorium is borne on the now irregularly swollen 'head' just below the tip of the hypocotyl, from the centre of the flattened side in contact with the host. At this stage the hypocotyl ceases to absorb water, withers from the base and disappears, this marking the end of the free-living phase. After a short time the attached part assumes an intense red colour.

After a resting stage of up to fourteen days slender shoots arise from the head and elongate rapidly. They nutate like the hypocotyl but more regularly, twining round the host and forming at intervals rows of adhesive disks from which endogenous haustoria reach to the vascular tissue, though without penetrating it (F.D.A. and B.V.). The haustoria secrete enzymes which facilitate penetration and break down intracellular materials.

If the seedling fails to find a host it is capable of living for just over three weeks. It falls to the soil and continues to increase in length at the expense of diameter. Normal seedlings reach 1·25–2·5 cm. in length (Mirande gives 3–4 cm.), but if no host is available they attain 3–4 cm. (Mirande gives 7–8 cm.) and 0·25 cm. in breadth. The seedling begins to wither from the radicle end but water absorption continues through the epidermis of the hypocotyl. The tip is still raised and continues to nutate. Attachment is still possible, and the tip is swollen and much thicker than the withered stem.

(*f*) *Effective reproduction.* In the writer's experience entirely by seed. Long (1910) mentions dodders being spread by small fragments of the stem and he quotes E. Marre as saying 'dodder may be spread by means of small tubercles which are formed in winter'.

IX. *Parasites, diseases, etc.* See *Cuscuta* L.

X. *History.* No fossil records appear to be known. The species was first noted as British by Gerard (1597).

C. europaea is very markedly erratic in its appearance, and in some years it is not to be found in its usual loci. There is a little evidence that the species undergoes a cycle of abundance. In Bedfordshire, for instance, a county which has been well and continuously botanised for over 150 years a survey of the records gives this impression. Abbot (1798) states that the plant was common in his day. There are only two records between that time and 1943 when the writer discovered the plant at Leighton Buzzard. In the past three years it has been discovered in three well-botanised parts of the R. Ouse. It is significant to add that recent dredging operations carried out in this river have led to the banks being piled with debris and nettles have increased enormously. During this period the plant was

noticeably commoner in many of its Surrey and Berkshire localities, in some of which river dredging has also been recently carried out, e.g. the R. Loddon. J. D. Grose states that similar increases have been noted in the Bristol Avon area. In 1937 it was definitely absent from part of the river near Staverton, but in 1941 it occurred in great abundance. Druce (*Comit. Fl.*) states that in 1932 it was 'decreasing'. Plotting all the available records against time has revealed no analysable information. A thorough knowledge of the biology of the germination would clear up many of the mysteries concerning this plant.

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Orchis purpurea Huds.

F. ROSE

Sect. MILITARES. A tall tuberous perennial, 20–100 cm. high. Tubers 2, ovate, 3–6 cm. long, that of the current year brown and withered at time of flowering, without roots at the apex, that for the next year turgid and ivory-coloured with a few unbranched fleshy
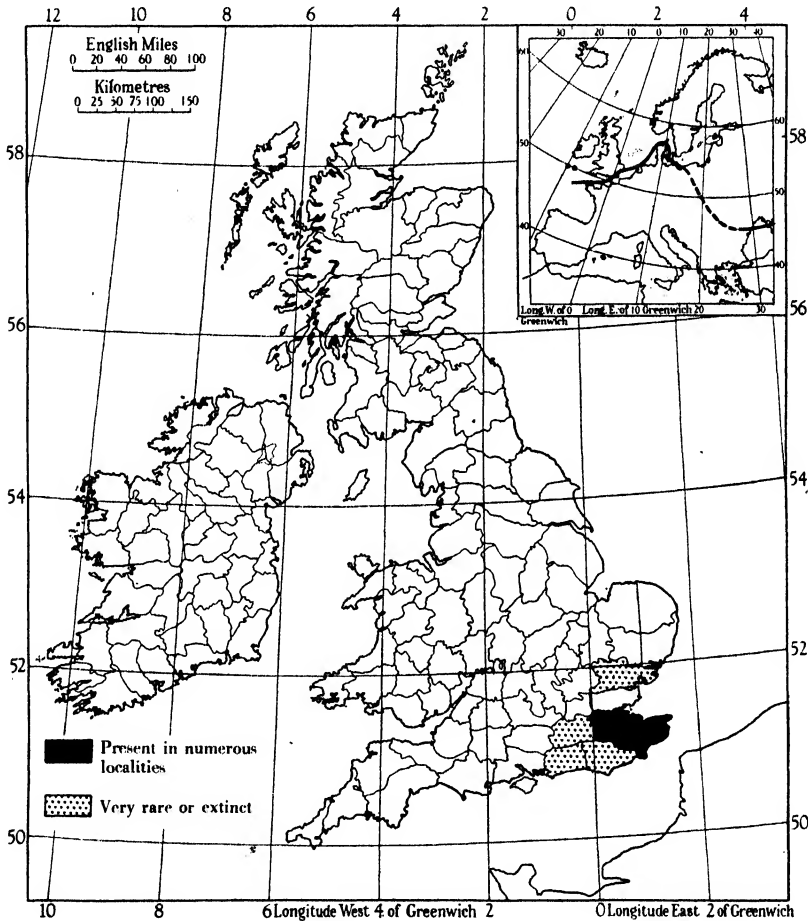

Fig. 1. *Orchis purpurea* Huds. Vice-comital distribution in the British Isles and (inset) northern limit in Europe.

roots without root-hairs arising in a circular crown from the apex. Stem stout, 0·4–0·9 (average 0·6) mm. in diam. Leaves large, 2–5 cm. wide, ovate-lanceolate, rather acute, with sheathing base, rather thin and soft, the upper stiffer, all brittle, deep shining green above, rather glaucous, with 10–20 darker veins below; lower leaves forming a basal rosette, upper successively more keeled and clasping, sometimes with a small leafy bract

above the uppermost leaf. In woodland plants the lower leaves are darker than the upper, while in plants from open scrub all the leaves tend to be paler, more obtuse and of firmer texture. Flowering raceme long and lax, or, in plants from open scrub, short and dense; bracts minute. Sepals 3, ovate, acute, forming a helmet over the stigma and anther, green throughout, but heavily flecked with small purple patches due to an anthocyanin pigment. Upper petal (actually the lowest, owing to the twisting of the pedicel) forming a pale pink or white labellum with numerous raised crimson papillae, each formed of acutely pointed cells with red sap, divided into narrow upper lobes, two broad squarish lower lobes and a short triangular median tooth. Spur pale pink, about half as long as the ovary. The two other petals narrow, strap-shaped, papillose like the labellum. Ovary about 2·5 cm. long, obovate-fusiform, green, glossy, bearing three longitudinal ribs. Fruit obovate, 2·5–3 cm. long, 0·5–0·7 cm. in diam., dehiscing by three longitudinal slits. Seeds very numerous, 0·5–0·7 mm. long, fusiform, consisting of a thin papery testa enclosing a central globular undifferentiated embryo of a few cells only.

Although very well-marked and stable species both in Britain and on the Continent, it shows much variation in the form and colour of the labellum, though only within certain limits. Besides the variation apparently due to the environment, there is much which is probably due to genetical factors. In the same locality colour variations may be found ranging from albinos with pure white lips and straw-coloured hoods to plants with deep purple hoods and pink-flushed lips heavily blotched with purple. The lip varies from a dagger-shaped type (this is very rare) and a broad, entire, crenate type, through those with two 'arms' or with both 'arms' and 'legs', to the other extreme with all four lip segments long, narrow and truncate and the central lobe or mediastin very evident. The last is the 'var. *pseudo-militaris*' of Druce, but it does not resemble *O. militaris* sufficiently to cause confusion to those familiar with the latter species. Camus (1929) lists numerous Continental varieties.

The writer has seen a peloric form, i.e. the two smaller petals in every flower had formed a lip, so that the flower was symmetrical and 3-lipped; only one anther, however, was developed in each flower.

No ecotypes are known, unless the two geographical races described below (I) can be regarded as such. Much of the colour variation seems to be environmental, as plants in the open are nearly always darker-flowered than those in the shade, with a tendency to brownish rather than purple marks on the flowers. A 'gigantic' form has been reported from rich meadowland off the chalk; this had a stem 2 cm. thick, leaves 27 cm. long and a bifurcated spike (Brooke).

A very local plant in Britain, confined to chalk scrub and beechwoods on chalk in the extreme south-east, where, however, it is still locally plentiful.

I. *Geographical and altitudinal distribution.* Found only in east Kent (15), west Kent (16), Surrey (17) and west and east Sussex (13 and 14). Formerly in north Essex (19) (Hall, 1935). Erroneously reported for Middlesex (21). Locally frequent in Kent on the downs on both sides of the Medway valley and locally abundant in eastern Kent between the Stour and Dover (Fig. 2). Still known in over ninety localities in Kent. In Surrey and Sussex now extremely rare and restricted at present to one station in each vice-county; latest reports suggest that it may in fact be extinct in Sussex (Bedford).

In Kent two separate centres of distribution occur: (i) the downs on both sides of the Medway valley and sporadically eastwards towards the Stour valley, (ii) the downs from

the east side of the Stour valley to a line from Wingham to Dover. In each of these areas the plant is found as a fairly well-marked geographical type, fairly constant respectively in the forty-five western stations and thirty-two eastern stations in which the plant has been observed by the writer. The western type has the following characters: height 8–15 in. (20–38 cm.), spike short and dense, ovary $\frac{1}{2}$–$\frac{3}{4}$ in. (1·3–1·9 cm.) long, labellum short, crimson spots prominent, anthocyanin pigments rose to purple. In the eastern type the plant is 12–30 in. (30–76 cm.) high, the spike long and lax, the ovary $\frac{3}{4}$–1 in. (1·9–2·5 cm.) long, the crimson spots usually less prominent, anthocyanin pigments salmon to brownish red.
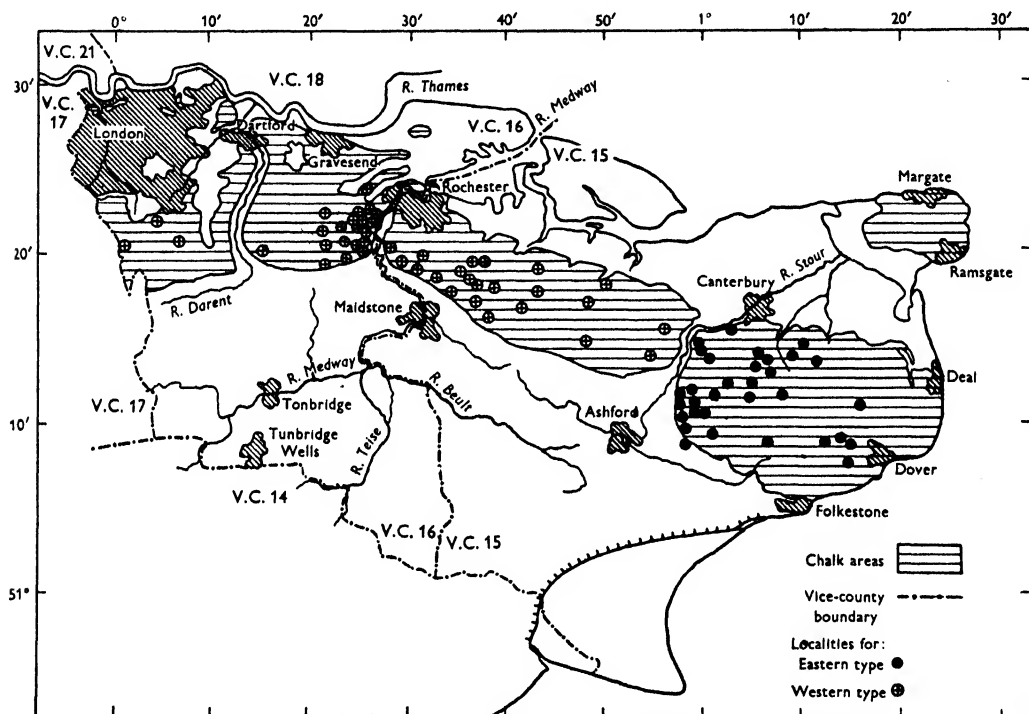

Fig. 2. Sketch-map of distribution of *Orchis purpurea* Huds. in Kent.

In western Europe *O. pupurea* is scattered sparsely through France, where it is locally frequent, to northern Spain, and occurs in the mountains of southern Spain. It is very rare in the Netherlands and north German plain and extends to Jutland, Möen, Rügen and Oesel, but not into Scandinavia. It occurs in a similar local manner through central Europe, but is rare in the Swiss and Austrian Alps. Extends south to Corsica and the mountains of central Italy, where it is abundant and is the commonest woodland orchid (Brooke). Missing large areas, such as Silesia, Poland and Galicia, it stretches sporadically eastwards into the mountains of Thrace, Rumania, the Crimea and Asia Minor. It is reported for central and south Russia,* but these isolated stations so far east are somewhat doubtful. It occurs in the mountains of Algeria and Tunisia (*Lebensg.* **1**).

In Britain it occurs between 200 and 700 ft. (10–200 m.).

* But given only for the Crimea in the *Flora U.R.S.S.* (Kanarov, 1935).

II. *Habitat*. In England this species is largely confined to two types of habitat:

(i) Dense chalk scrub or coppice, where it gets moderate light, but also the shelter from grazing animals, extreme dryness and wind which it seems to need. (ii) The lower edges of chalk escarpment beechwoods, where it usually grows on the terraces formed by the surface roots of the beeches, or else on the crests of chalky banks in these woods. It avoids deep hollows where much leaf humus collects, such as those preferred by *Neottia nidus-avis*. Though mostly occurring on south-facing slopes, it is not restricted to them and prefers moderately deep shade, but often occurs just outside woods.

Thus, although *Orchis purpurea* occurs in similar habitats to *O. militaris*, its usual habitats contrast with those of the two other British Militares (*O. simia* and *O. ustulata*) which in this country almost always occur in open grassland. *O. purpurea* occurs on open downs, but rarely, and does not seem to flourish there. After much experience of the plant in many localities the writer thinks it probable that the original habitat of the species in Britain was chalk scrub, for two main reasons: (i) It is always more at home and more plentiful in scrub than in beechwood; indeed in the latter habitat it is always rather scattered and does not flower very freely. (ii) The hazel and other chalk shrubs under which *O. purpurea* grows most happily are known from peat records to have existed in England before the beech. We can, indeed, see the invasion of the beech still occurring at the present moment in the localities concerned.

The soils on which *O. purpurea* is found overlie the Middle and Upper Chalk and show typical Rendzina profiles, permanently immature. A layer of dead leaves often occurs on the surface. Stable humus formed from this occurs below and merges gradually into fine soil, formed from weathered chalk mixed with humus and lumps of chalk; this in turn merges into chalk rock at a depth of 6 in. to 1 ft. (15–30 cm.). In east Kent stations it has been noticed that the soil is often slightly deeper; this may be connected with the higher rainfall. The soil is very rapid-drying, owing to its porosity, and the water-table is very deep. Worms are usually plentiful. The humus decays fairly rapidly (in about a year) and is dense, black and finely divided. The profile is alkaline throughout; pH 8·0–8·3 at the surface, 8·5 at 4 in. (10 cm.) rooting depth and 7·0–7·5 in the loose humus, seem to be typical values.

III. *Communities*. The species in its most usual type of habitat, occurs in a community of shrubs, of which the following is a typical list:

Cornus sanguinea	a.-co-d.	Prunus spinosa	f.-a.
Corylus avellana	a.-co-d.	Rosa spp.	f.-a.
Crataegus monogyna	a.	Sorbus aria	f.-d.
Euonymus europaeus	o.-a.	Viburnum lantana	a.
Ligustrum vulgare	f.-a.		

The ground layer is often very open, but is usually dominated by *Mercurialis perennis*, which is the most constant and characteristic associate of *Orchis purpurea* in Britain. In the beechwood type of habitat the ground between the plants is often bare of other vegetation and covered only with fallen beech leaves. The beechwoods in which the species occurs, however, are usually of the '*Mercurialis*' type, on deeper soils and less steep slopes than the '*Sanicula*' type. In the two Kentish areas mentioned the constancy of the species is very high, both in such woods and in scrub, at least locally.

Apart from *Mercurialis perennis*, there are four other very characteristic associates of *Orchis purpurea* in certain west Kent localities, viz. *Helleborus foetidus* f.-a. (but of low

constancy), *Daphne laureola* f.-a. (high constancy), *Iris foetidissima* l.a.-l.d. (high constancy), *Primula vulgaris* v.a.-l.d. (high constancy).

Details of the communities in a number of localities in which *Orchis purpurea* occurs are given below. The localities are referred to by numbers; the first column represents seven quadrats (area 1 sq.m.) in a west Kent locality. The figures indicate the number of individuals per quadrat:

	I Foot of ash	II Near beech	III By beech	IV Near yew	V On a bank	VI	VII
						Open ground beneath beeches	
Ajuga reptans	—	4	—	1	—	—	—
Arum maculatum	1	5	—	—	—	—	—
Calamintha ascendens	3	1	—	—	—	—	—
Euonymus europaeus	1	5	—	—	—	—	—
Euphorbia amygdaloides	1	—	—	—	1	—	—
Glechoma hederacea	—	9	—	—	—	—	—
Helleborus foetidus	—	—	—	—	1	—	—
Hypericum perforatum	2	—	—	1	2	—	—
Iris foetidissima	—	6	—	—	—	—	—
Mercurialis perennis	2	6	3	12	13	—	—
Orchis purpurea	1	1	1	3	1	5	3
Ranunculus bulbosus	2	—	—	—	—	—	—
Taraxacum sp.	1	—	—	—	—	—	—
Taxus baccata (small)	—	1	—	—	1	—	—
Teucrium scorodonia	—	5	—	—	—	—	—
Viola riviniana	—	—	—	4	—	—	—

and the following bryophytes:

	I	II	III	IV	V	VI	VII
Barbula convoluta	—	—	—	f.	—	—	—
B. unguiculata	—	—	—	f.	—	—	—
Brachythecium rutabulum	—	—	—	—	a.	—	—
Camptothecium lutescens	a.	f.	—	—	—	—	—
Eurhynchium crassinervum	f.	—	f.	a.	f.	o.	—
Hypnum cupressiforme	—	—	—	—	a.	—	—
H. molluscum	—	—	—	—	a.	—	—

In the west Kent station, loc. W 22, the species occurs in a copse on Upper Chalk, in the bottom of a 'dry' valley in the heart of a large wood. Here the shrub layer contains the following (1944):

Acer campestre }	co-d.	Euonymus europaeus	a.
Corylus avellana }		Ligustrum vulgare	o.-f.
Crataegus monogyna	a.	Malus pumila	o.
C. oxyacanthoides	v.r.	Viburnum lantana	a.-l.d.

The herb layer in this copse appears in two separate facies which seem constant, due to small local variations in soil moisture. *Orchis purpurea* is absent from the drier facies, which has:

Listera ovata	v.a.	Scilla nonscripta	v.a.
Mercurialis perennis	d.	Viola riviniana	f.
Porotrichum alopecurum	o.		

The wetter facies, which contains *Orchis purpurea*, has:

Aceras anthropophorum	o.	Orchis mascula	o.-f.
Ajuga reptans	v.a.	Orchis purpurea*	f.-l.a.
Arum maculatum	f.	Plantanthera chlorantha	a.
Cephalanthera damasonium	f.	Primula vulgaris	v.a.-l.d.
Clinopodium vulgare	a.	Ranunculus repens	o.
Epilobium obscurum	f.	Rubus (?) rusticanus	f.-a.
Glechoma hederacea	f.-a.	Scilla nonscripta	l.f.
Listera ovata	a.-l.v.a.	Veronica chamaedrys	a.
Ophrys muscifera	l.f.	Viola riviniana	a.-l.d.

* Fifteen seen with flower spikes, three rabbit-injured, about an equal number without.

and the following bryophytes:

Brachythecium purum	o.	Hylocomium triquestrum	l.d.
Eurhynchium striatum	l.a.	Porotrichum alopecurum	l.d.
E. piliferum	l.a.	Thuidium tamariscinum	l.f.

W 16 is another similar habitat in west Kent. Here the species grows in a very limited area of chalk copse; the chalk is only exposed here as a small outcrop, near the edge of a large wood of which the subsoil is mostly Thanet Sand, with coppiced *Castanea* and locally *Carpinus* as the chief dominants.

The soil where our plant occurs is loose chalk debris, with scarcely any loam.

In the copsewood, which appears to have formed by direct colonization of grassland, are the following:

Acer pseudo-platanus	f.	Corylus avellana	co-d.
Castanea sativa	o.	Rosa canina	f.
Cornus sanguinea	co.-d.	Viburnum lantana	co-d.

Field layer:

Aceras anthropophorum	f.	Orchis mascula	o.
Ajuga reptans	f.	O. purpurea	f.-l.a.
Arum maculatum	f.-a.	Poa nemoralis	o.
Daphne laureola	o.	Potentilla reptans	l.a.
Fragaria vesca	a.	Primula vulgaris	v.a.-s.d.
Galeobdolon luteum	f.-a.	Scilla nonscripta	f.
Listera ovata	f.-a.	Tamus communis	f.
Lonicera periclymenum	f.	Taraxacum officinalis	(agg.)
Mercurialis perennis	sparsely d. (ground rather bare)		
Myosotis arvensis	r.	Viola riviniana	a.
Ophrys insectifera	f.-l.a.		

In one year fourteen plants flowered, the next year three only; the numbers not flowering were approximately forty and fifty respectively.

Ruscus aculeatus is very often locally dominant in the woods where *Orchis purpurea* occurs, but never seems to grow with it; it seems to occur mostly at the upper edges of the chalk areas, at the junction of the sand.

In another locality, W 5 (v.c. 16), by far the best surviving locality for the 'western' type, the species occurs in thick chalk scrub dominated by *Sorbus aria*; this is a stage in a sere between chalk grassland and beechwood and the bushes are young (c. 3–6 m. high). The light intensity here is higher than usual, as *S. aria* casts only a light shade. *Orchis purpurea* is locally very abundant (about 300 plants were estimated to be in flower here in May 1944 in an area about 50 × 20 m.). *Valeriana officinalis* is locally frequent to locally abundant. Other species present are: *Tamus communis, Clematis vitalba, Ajuga reptans, Glechoma hederacea, Primula vulgaris, Festuca rubra, Fragaria vesca, Pimpinella saxifraga,* etc., and the following orchids: *Aceras anthropophorum, Herminium monorchis* (at open wood border only), *Ophrys insectifera, Orchis mascula.*

In locality W 2, a beechwood habitat in west Kent, the associates of *O. purpurea* are: *Aceras anthropophorum, Atropa belladonna, Cephalanthera damasonium, Neottia nidus-avis, Ophrys insectifera, Orchis mascula* and *Sanicula europaea.* No one species is dominant in the field layer. The bryophytes present are *Barbula unguiculata, Brachythecium purum, Camptothecium lutescens, Madotheca platyphylla, Neckera crispa* and *Thuidium hystricosum.*

Locality W 2 is interesting in that it resembles certain localities in the Vexin Français (France) described by Allorge (1922) (see below). *Orchis purpurea,* nevertheless, seems very healthy here, up to fifty flowering plants appearing over perhaps 50 sq.m. in good years.

The following notes refer to four localities for the 'eastern' type. The rather bare beechwood type of habitat is less frequently found in Kent east of the Stour, the chalk woods being mostly more mixed, with a richer ground flora. Here *O. purpurea* is usually found just inside such woods, in the copsewood of calcicolous shrubs which usually forms their border.

In locality E 13 the plant occurs at the edge of a wood in a 'dry' valley, where *Viburnum lantana*, *V. opulus*, *Acer campestre*, *Cornus sanguinea*, *Fraxinus excelsior*, *Euonymus europaeus*, *Coryllus avellana* and *Rosa canina* are all abundant to co-dominant. Higher up the valley side, where drift overlies the chalk, *Carpinus betulus* is the dominant, and the writer has never observed *Orchis purpurea* under this tree. *O. purpurea* is very abundant in this locality and is associated with several species not seen in the west Kent localities examined; these are included in the following list:

Ajuga reptans	l.a.	Melandrium dioicum	l.f.
Allium ursinum	l.d.	Mercurialis perennis	a.-l.d.
Arctium minus	r.	Paris quadrifolia	a.-l.d.
Galeobdolon luteum	f.	Primula vulgaris	f.
Hedera helix	a.-l.d.	Sorbus aria	o.
Hypericum hirsutum	f.	Tamus communis	a.
Melampyrum pratense	a.-l.d.	Viola reichenbachiana	a.

and the following bryophytes:

Anomodon viticulosus	l.f.	Hypnum cupressiforme	a.
Hylocomium triquetrum	l.a.	Porotrichum alopecurum	a.-s.d.

The orchids here are:

Listera ovata	a.	O. mascula	f.
Orchis maculata	f.	Platanthera chlorantha	l.a.

The soil is a well-developed Rendzina, deep and moist, with plenty of alkaline humus over the chalk rock, which is 15–20 cm. below the surface. The light intensity is low in the wood, and the humidity high even in summer. *Orchis purpurea* also occurs just outside this wood, in grassland with:

Bromus erectus	d.	Hippocrepis comosa	a.
Gymnadenia conopsea	a.	Orchis maculata	f.

The plants here are smaller and darker-flowered.

At locality E 14 our plant occurs at the edge of *Cornus-Viburnum lantana* scrub with the following orchids: *Platanthera bifolia*, *P. chlorantha*, *Ophrys insectifera*, *Aceras anthropophorum*, *Orchis mascula*, *O. maculata*, *Cephalanthera damasonium*, *Epipactis helleborine*.

In locality E 15, typical of many others, *Orchis purpurea* grows in copsewood of pure hazel, with *Mercurialis perennis* thickly dominant. Here the soil is deep and rich in humus; *Monotropa hypopithys* is frequent.

In yet another east Kent locality *Orchis purpurea* occurs in great abundance, and attains a large size (up to 80 cm.) in a damp wood on Gault Clay at the foot of the chalk downs. Plentiful chalk down-wash and the presence of chalk springs render the soil here a marl rather than a clay; the pH is over 8·0, and the soil gives a vigorous effervescence with HCl. The wood consists of dense hazel coppice, with occasional standards of *Quercus robur*. *Cornus sanguinea*, *Fraxinus excelsior* and *Euonymus europaeus* are frequent in the shrub layer, while the ground layer contains:

Anacamptis pyramidalis	f.	Ophioglossum vulgatum	o.
Carex pendula	l.a.	Ophrys insectifera	f.
C. sylvatica	f.	Orchis mascula	f.
Cephalanthera damasonium	o.	Paris quadrifolia	a.
Galeobdolon luteum	l.a.	Platanthera chlorantha	f.
Mercurialis perennis	d.	Pyrola rotundifolia	l.f. (formerly)

The light intensity is very low for most bryophytes; *Eurhynchium striatum* (l.d.) and *Hylocomium triquetrum* (l.a.) are the only prominent species.

On the Continent Allorge records *Orchis purpurea* as a rare plant in calcareous grassland in the Vexin Français (an area in the Paris basin). This grassland is dominated by *Festuca duriuscula (rubra?)*, *Bromus erectus*, *Brachypodium pinnatum* and, more locally, *Koeleria critata* and *Sesleria coerulea*. *Ophrys arachnites* occurs also, but is rare. *Orchis purpurea* is frequent in a community with *Brachypodium pinnatum* dominant. Perhaps most interesting, from our point of view (compared with these non-British habitats), is the record of *Orchis purpurea* as one of the very few angiosperms found under very dense scrub of *Prunus spinosa* and *Crataegus monogyna* on calcareous soils (the others are *Ophrys insectifera*, *Geranium robertianum* and *Helleborus foetidus*) as scattered individuals in a mossy carpet. If *Cornus* and *Viburnum lantana* were added to the shrubs and *Aceras* to the field layer, the description would be identical with that of some west Kent localities, such as W 18 and W 22.

In the Limmattal (Switzerland) Scherrer (1925) records *Orchis purpurea* in a community dominated by *Molinia caerulea* var. *littoralis* and *Brachypodium pinnatum*, with occasional shrubs, such as *Prunus spinosa*, *Ligustrum*, *Viburnum lantana*, *Frangula alnus*, *Berberis vulgaris* and *Pinus sylvestris*. This community is on rather more calcareous slopes, with a more water-retentive tendency, than a dry grassland community, dominated by *Bromus erectus*, in which *Ophrys arachnites* occurs, but *Orchis purpurea* is absent.

IV. *Response to biotic factors.* In a west Kent locality (W 13), besides occurring in beechwood, *O. purpurea* is found in a clearing where the beeches and other trees were mostly blown down in a blizzard some years ago. Here many plants often found in such clearings have colonized the space, mostly chalk species, but including some species not usually found on chalk. *O. purpurea*, however, seems quite happy, possibly because it still gets the wind shelter it seems to like, and more light than it did before.

A list for a typical quadrat is appended (numbers refer to the number of individuals of each species):

Ajuga reptans	1	Mercurialis perennis	v.a.
Cirsium lanceolatum	1	Orchis purpurea	3 (2 in flower)
Clematis vitalba	2	Primula vulgaris	1 seedling
Crataegus monogyna	1 seedling		4 clumps
Epilobium angustifolium	10	Ribes rubrum	1
E. montanum	3	Rubus rusticanus (?)	2
Fragaria vesca	a.	Viburnum lantana	1.

Near by, in the same area with *Orchis purpurea*, were: *Aquilegia vulgaris*, *Atropa belladonna*, *Betula pubescens*, *Brachypodium pinnatum*, *Daphne laureola*, *Dryopteris filixmas*, *Euphorbia amygdaloides*, *Inula conyza*, *Ligustrum vulgare*, *Lithospermum officinale*, *Pteridium aquilinum*, *Rosa canina*, and *Salix caprea*.

Trampling destroys the delicate leaves and brittle stem and, if on a large scale, would soon destroy the species; luckily this is unlikely to occur in the spots where it grows. Plucking seems to do less harm than is often supposed, as a rule merely preventing the plant from fruiting, but, if at all heavy, soon tends to exterminate it. This is happening in a few places near main roads and villages and has already occurred in old stations near Dartford.

Rabbit nibbling is one of the most serious threats to the continued existence of the plant. In many localities a visit in late May or early June finds all, or nearly all, the spikes eaten or smashed off. At locality W 21, in April 1944, about eighty plants looked likely to flower; only fifteen were seen actually in flower in mid-May, rabbits having eaten

the rest. Leaves of many plants appear nibbled; the damage is even worse in the more open habitats. It may be remarked that rabbits are usually regarded as being largely responsible for the near extinction of *Orchis simia* and *O. militaris* in the Chilterns.

V. (*a*) *Gregariousness.* The species occurs mostly in small scattered colonies, sometimes as single plants. In certain localities it is locally very abundant and then occurs in scattered communities of groups of one to four plants (mostly singly), about 20–100 cm. separating each group. In some spots, 'good' years may produce 300–400 spikes; in other years there may be only a tenth of that number.

(*b*) *Performance in various habitats.* Average height in west Kent, 12–15 in. (30–40 cm.); in east Kent, 15–24 in. (40–60 cm.). The height is always less in the open.

Remarks have been made already on the variation in numbers of flowering individuals from year to year. This is a characteristic of most of the Orchidaceae in Britain. *O. purpurea* shows it less strongly than some species, as one or two flowering spikes nearly always appear except in the weakest colonies. A few figures on performance collected by the writer in various stations are appended:

Number of plants flowering

Locality	1936	1937	1938	1939	1940	1941	1942	1943	1944	1945
W 2	3	0	3	4	—	3	4	2	—	3
W 3	—	—	—	—	—	1	0	—	3	0
W 5	—	—	—	—	—	—	—	—	250	40
W 6	—	—	—	—	—	—	0	1	3	—
W 10	—	—	0	—	—	0	2	0	0	0
W 12	—	—	—	—	—	—	20	15	5	2
W 13	—	—	—	—	—	—	—	10	4	10
W 16	—	—	—	—	—	—	—	—	140	3
W 21	—	—	—	—	—	—	—	—	15	3
W 22	—	—	—	—	—	—	29	—	50	30
E 13	—	—	—	300	20	—	—	—	—	60
E 14	—	—	—	30	—	—	—	—	—	—

— indicates no observations made.

Owing to war conditions, these figures are far from complete. It seems, however, that 1939, 1942 and 1944 were 'good' seasons, the rest indifferent. 1939 was a 'good' year for most orchids; in fact, the majority of species have not had one since (written in 1945); *O. purpurea* is one of the few exceptions to this.

(*c*) *Effect of frost, drought, etc.* In the shelter of the woods, frost and drought affect the plants little, if at all; in open spots, however, the leaves and flowers become 'scorched' in cold springs, and the leaves are often yellowed and unhealthy. It may be remarked here that, as *O. purpurea* is a plant apparently as much at home in north and central Italy as anywhere else, where the winter and spring are cool and wet and the summer extremely dry and sunny, such a combination of conditions may be the cause (or at least one cause) of 'good' seasons in this species. Certainly 1943–4 were seasons showing an approach to the type described, while the summers of 1938 and 1941, preceding good years, were dry. There is, of course, as yet insufficient evidence on these and other problems, but they are worth study. It certainly seems likely that our plant at least does not suffer, and *may* benefit, from having its tubers dried out in summer in the shallow porous soil.

VI (*a*) *Morphology, etc.* Each plant has at the time of flowering two ovate tubers, 1–2 in. (2·5–5 cm.) long, one of which bears the current year's flowering stem and leaves, while the other will provide the shoot for next year. On the tuber for next year are borne

the 10–20 fleshy unbranched roots, which bear no root hairs. These spring in a rosette from the apex of the tuber. Also at the apex of next year's tuber is the bud of pointed fleshy scale leaves which will form next year's stem.

The tubers are from 2 to 6 in. (5–15 cm.) deep, usually about 4 in. (10 cm.), the depth depending on the depth of the soil. The roots grow radially outwards and downwards, and are 3–8 in. (8–28 cm.) in length.

(b) *Mycorrhiza.* Always present in the roots of all *Orchis* species so far examined and seems essential to the development and mature life of the plant. The fungal species is not recorded, but in the case of all orchid roots so far examined, except one Japanese species, the genus of fungus is the same, i.e. *Rhizoctonia* Bernard (*Orcheomyces* Burgeff) (Ramsbottom, 1922).

Recent work on orchid mycorrhiza, however, tends to a view differing from that usually held. Ten species of *Rhizoctonia* were isolated from twenty-three species of orchids from various habitats in the U.S.A. and Central America. No evidence of specificity was found, as one orchid species could harbour several species of fungus, and any one fungus species could attack several species of orchid. The fungi were correlated with ecological habitat rather than with the species of orchid. Symbiotic germination tests, using fungi isolated from a given orchid in combination with the seeds of that orchid, indicated in most cases that the fungi were unable to induce seed germination. The symbiotic relationship is considered to be one of parasite and host, with the orchid deriving no benefit from the fungus at its roots.

(c) *Perennation; reproduction.* Tuber geophyte. Perennates during the winter by the tuber formed during the previous spring. When the leaves appear above ground in February, they begin to produce the materials for the tuber of the year following; this probably means that the performance of the plant is affected less by the climatic conditions of the current year than by those of the previous spring.

Vegetative reproduction is of little importance, but occurs to a slight extent, as is shown by the occasional presence of two or three plants in a very close group. It is brought about when two new tubers, instead of one, are formed in the same season.

There are no precise figures for longevity, but since young plants take several years to mature the length of life is not likely to be normally less than 10 years. The age at first flowering in most species of *Orchis* is about 10 years (Webster, 1899). Sometimes flower spikes are produced in two consecutive years, as is proved by the occasional presence of last year's dead stem beside this year's flower spike. This was observed in 1945 in localities W 13 and W 16; two such plants were noted at W 13 and one at W 16. So of our native orchids *O. purpurea* at least is not essentially monocarpic. In most cases, however, it seems likely that the plant rests for a few years before flowering a second time; most plants bearing last year's dead stem do not flower in the current year.

(d) *Chromosome number.* 2n = 42 (Heuser, 1939; Hagerup, 1938. Material from Switzerland and Denmark respectively).

VII. *Phenology.* Maximal growth of roots, January to April; of tubers, February to June. Leafy shoots appear from mid-January to mid-February.

The usual flowering season is mid-May to early June, but in 1943 a plant was observed almost in flower on 11 April, and in 1945 most colonies were in full bloom by the first few days of May. Capsules mature in August and dehisce in September. Germination in nature not observed.

VIII. (*a*) *Floral biology.* Insect-pollinated, by small flies, also, at least on the Continent by small bees. Pollination mechanism as in the other species of *Orchis*. In Kent a fly, *Odyneras parietum*, has been observed to visit this species and to avoid *Orchis mascula* (Godfery, 1933). A hive bee has been seen visiting the flowers and withdrawing pollinia from this species and *O. simia* in France (Godfery, 1933).

This and other Orchidaceae are remarkable for their imperfect fertilization in this country and to a lesser extent on the Continent. This fact may help to account for the very local occurrence of the species. Ten fine spikes were sent to Darwin from two south Kent localities with most of the flowers partly withered and with the pollen mouldy even in the uppermost flowers; hence no more pollinia would be likely to be removed. Darwin examined two of these spikes fully and of sixty-two flowers only eight had had one or both pollinia removed, and only three had had both removed. The ten spikes bore a total of
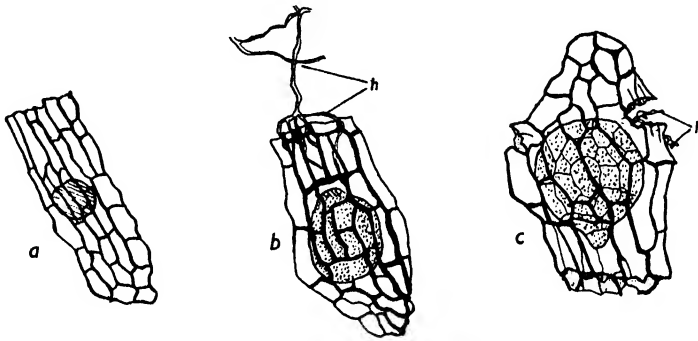

Fig. 3. (*a*), seed of *Orchis purpurea*. (*b*) and (*c*), ditto, after growth on soil in contact with fungus on roots of a mature plant. Fungal infection has occurred, and germination is commencing. *b*, after 7 days; *c*, after 20 days; *h*, fungal hyphae.

358 flowers, and of these only eleven had set capsules, five of the ten spikes having set not a single capsule. Godfery (1933) observed one spike near Wye (Kent) with both pollinia removed from the four lowest flowers, but other spikes examined had no pollinia removed.

This imperfect fertilization is probably due to the plant's not being sufficiently attractive to insects. It is less marked on the Continent; Sprengel (in Darwin, 1904) noted five spikes of the closely allied *O. militaris* with 138 flowers which had set thirty-one capsules.

The flowers are almost certainly amphimictic; cleistogamy has not been observed and is not likely to occur.

(*b*) *Hybrids.* No hybrids have been observed in Britain, but on the Continent hybrids with *O. militaris* and *O. simia* have been reported (Aschers. & Graebn. **3**).

(*c*) *Seed production and dispersal.* Darwin found that a capsule of *O. maculata* which he examined contained 6200 seeds; since the capsules of *O. purpurea* are about twice the volume and the seeds appear about the same size, probably about twice as many seeds per capsule are produced as in *O. maculata*. The number of capsules produced is, as stated, very variable.

The writer's own observations suggest that, in some years at least, fertilization is not always as imperfect as suggested by Darwin's observations quoted under VIII (*a*). In 1943, at two stations, one in west and one in east Kent, several plants were seen with six or seven capsules set on each. Certainly the species does not appear to be diminishing at the present moment, and may even be slightly increasing its numbers.

Capsules are loculicidal, with longitudinal slits; the seeds are small and light as fine sawdust, and are wind-dispersed.

(d) *Viability of seeds; germination.* The viability of the seeds must be extremely low, as they have no protective coat or food reserves, and consist only of a thin, spindle-shaped envelope with an undifferentiated embryo of a few cells inside.

Germination is difficult to obtain under laboratory conditions. Seeds collected in October 1947 were sown after an interval of 4 months in February 1948, on chalky soil round the partly exposed roots of a mature plant, growing in a flower pot. The pot was kept in an incubator in the dark at 25° C. and watered regularly. Fungal infection of the seeds occurred, and the early stages of germination following infection were observed (see Fig. 3). No development occurred in uninfected seeds.

(e) *Seedling morphology.* No seedlings seen.

(f) *Effective reproduction.* Almost entirely by seed (see VI(c)).

IX. (a) *Animal feeders or parasites.* No insect or other pests have been observed by the writer; snails, however, certainly do much damage to the leaves and stem.

(b) *Plant parasites.* No information.

(d) *Diseases.* No information.

X. *History.* No information; the extreme south-east distribution in Britain suggests fairly recent immigration from the Continent.

First recorded as British by C. Merrett (*Pinax Rerum Naturalium Britannicum*, 1666, p. 87); apparently either he or John Goodyer, the Cavalier botanist, found *O. purpurea* near Gad's Hill, near Gravesend—possibly in the spot where it still flourishes at the present day.

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